

THE MARINE ENOPLIDA
(NEMATODA) : A COMPARATIVE
STUDY OF THE HEAD



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SYNOPSIS

This report is based on a collection of free-living marine nematodes from South African waters and is in two parts. The first part deals with the comparative anatomy of the head in the marine Enoplida and the second presents some comments on the classification of this group with the description of twenty-four species, of which twenty-two are named as new, belonging to eighteen genera, of which four are new. The species and genera treated are listed on page 300. The presence of a zone of fusion between the oesophagus and the body wall is characteristic of the families Phanodermatidae, Enoplidae and Leptosomatidae and it is argued that this is primitive and represents one of the major reasons for the evolutionary success of this Order of nematodes. The more specialized head forms in the same families are characterized by the presence of a fluid filled space at the anterior end of the body, the cephalic vesicle, the functional significance of which is discussed. It is the development of this vesicle which explains the appearance of many of the characteristic structures of the head. Thus, in the Phanodermatidae the presence of six rods in the lining of the buccal cavity appears to be common and they occur in *Phanoderma*, *Dayellus* gen. nov. and—what can be interpreted as homologues—in *Crenopharynx*. These rods and the mandibles in the Enoplidae always lie in close relationship to the nerves which supply the labial sense organs and it is argued that they have arisen as supporting structures. In the Enoplidae it is shown that the head structures represent components in a functionally interrelated complex and that mandibles of forms such as *Enoplus* represent the fusion and condensation of an elaborate system of diverse structures. The “mandibles” arise from two sources, one anterior to the oesophagus, the buccal cavity, and one in the anterior end of the oesophagus itself, the onchial cavity. The buccal cavity component represents three structures, a median plate of thickened cuticle and two flanking rods—which are probably homologous with the buccal rods of the Phanodermatidae. The onchial cavity component represents a plate of thickened cuticle developed in association with the three large onchia characteristic of many groups of this family and it is on this plate that all the specialized musculature at the anterior end of the oesophagus is inserted. No musculature is inserted on the mandibular—or buccal cavity—component. The structures derived from these two sources in some cases fuse, as in *Mesacanthion*, but the original components can still generally be made out. The onchial plate is extended as narrow arms towards the radii of the oesophagus and the onchial: mandibular complex is slung by these arms so that it can rotate around a line lying between two rings of specialized anterior oesophageal musculature. This musculature is so arranged that contraction of the anterior ring causes the mandibles to open and contraction of the posterior ring acts in apposition. In the Leptosomatidae the head is characterized by the oesophageal musculature passing anteriorly through the cephalic vesicle so that the buccal cavity is always small and no structures develop in the wall of the buccal cavity to support the sense organs. Structures comparable to buccal rods, but probably of little evolutionary importance, are developed on the anterior edge of the cephalic capsule in forms such as *Parabarbonema* and *Thoracostoma*. In the Oncholaimidae no trace of the cephalic vesicle can be found but in *Pontonema*, at least, the remains of a cephalic capsule are present and it is argued that the large mouth capsule in this family is an enlarged onchial cavity and that the buccal cavity has been lost or almost completely suppressed. It is suggested that the Phanodermatidae, Enoplidae and Oncholaimidae represent a group of related forms separate from the Leptosomatidae and possibly the Oxystomidae and Ironidae, which probably represent another group of related forms. The Eurystominae and Enchilidiinae probably arose from the first line but are almost certainly not themselves closely related. From this it follows that in the first group of families there has been a series of evolutionary changes from mouth openings bounded by three lip-lobes to those with six lip-lobes then to three large lips and finally six lobes again or even no lip-like structures at all. The argument is advanced that to attempt to derive the various forms of the mouth structures in the Nematoda as a whole from one simple form is a mistake since they appear to represent the expression of independently acquired structures developed from an extremely labile region. Thus the term lip has only descriptive significance and can carry no indication of homology. It has been necessary to

introduce a number of morphological terms and these are listed, with definitions, on page 296. Among the taxonomic observations made the following are worthy of special note: *Thoracostomopsis* Ditlevsen, 1919, is a typical member of the Enoplidae and the so-called spear in the mouth is composed of three long, thin wholly cuticular onchia. The present classification of the families Enoplidae and Leptosomatidae is most unsatisfactory as there are probably several evolutionary lines classified horizontally within them. In particular the delimitation of the genera *Enoplolaimus*, *Mesacanthion* and *Enoploides* is unsatisfactory. Because of the difficulty involved in studying this satisfactorily no changes have been proposed in the classification but attention is drawn to the apparent weaknesses. The Superfamily Tripyloidea is not accepted but, because almost all the criticism offered is destructive, it is suggested that the classification of the Order used by Wieser (1953), that is to families only, should continue in use.

INTRODUCTION

THE marine representatives of the Nematode Order Enoplida were first adequately treated by Filipjev (1916) and later (1927) in "Les Nématodes libres des mers septentrionales appartenant à la famille des Enoplidae" the foundation of what is now treated as at least a Suborder was laid down. Filipjev (1934) presented the first reasonable classification of the Nematoda as a whole, a classification which Chitwood later (1933, 1937, 1937a and 1950) modified. This modified version has been accepted for some time although there have been various criticisms of it, notably that of Hyman (1951). However, it has become increasingly clear that the Chitwood classification is unsatisfactory until Chitwood (1960) can say "... the classification of the Nematoda is at present in no condition to be stabilized ..." and later he (1962) and Goodey (1963) have, rightly, accepted that his division of the Nematoda into two major groups can no longer be accepted. Comments on the classification of the marine Enoplida have been made at various times by a variety of authors, De Coninck, Gerlach, Schuurmans Stekhoven and Wieser in particular. Most recently Clark (1961) has published a "Revised classification of the Order Enoplida", which he modified slightly later (1962). In spite of the passage of more than thirty-five years Filipjev's 1927 classification of the marine Enoplida has remained essentially unaltered although most of his subfamilies are now treated as families. Thus the Superfamily Enoploidea of Clark contains the same groups as were included in the family Enoplidae by Filipjev, with the addition of a few groups discovered since Filipjev's publication. Further, Filipjev, most clearly in 1934, separated the Enoplidae as containing those forms with "Cuticle with duplication on the head" and this character is used by Chitwood (1950) and by Clark (1961) in delimiting the Superfamily Enoploidea. In spite of the classification of the marine Enoplida being based largely on the structure of the head it has never been adequately analyzed. Even Wieser's (1954) treatment of the Leptosomatidae is incomplete. Such an analysis is an urgent requirement and, although I have previously been able to make some isolated observations on the structure of the head in some genera of the Enoplida (*Trissonchulus* (Inglis, 1961), *Enoplus*, *Phanoderma*, *Oncholaimus*, *Prooncholaimus*, *Symplocostoma* and *Eurystomina* (Inglis, 1962) I had been unable to study any wide range of head structure when Professor J. H. Day, University of Cape Town, Republic of South Africa asked me to look at the free-living marine nematodes collected by the Ecological Survey of the

Department of Oceanography of that University. As a result of studying these specimens I have been able to work out the structure of the anterior end in a wide number of different forms, particularly forms with so-called mandibles (i.e. Enoplidae sensu Wieser) and am able to describe the comparative morphology of the head and to discuss the functional demands which have, to some extent at least, determined it. The most immediate result is to complicate the taxonomy : almost certainly because of insufficient information about the groups under consideration.

This report is in two parts. The first part deals with the structure of the head, particularly in the family Enoplidae—this is a result of basing the study on a general collection and simply represents the dominance of this family in the samples—and the second gives descriptions of the species studied with some observations on the classification of the marine Enoplida.

THE STRUCTURE OF THE HEAD IN THE MARINE ENOPLIDA

INTRODUCTION

The most immediate, and long standing, errors in the interpretation of the structure of the head in the marine Enoplida are the misunderstanding of the so-called "doubled cuticle" and the reference to the mandibles of the Enoplidae as consisting, in many forms, of pillars connected anteriorly by bars. The "doubled or duplicate cuticle" of the head is the result of the presence of a fluid filled space at the anterior end of the body, which I propose to call the *Cephalic ventricle*, the origin of which has been misunderstood by Filipjev. The only attempt to describe this structure is that of Filipjev (see Filipjev and Schuurmans Stekhoven (1941)) where he shows the outer cuticle of body curling in to the mouth opening and running backwards to rejoin itself posterior to the anterior end of the oesophagus, thus forming a pocket at the anterior end of the body. This interpretation is not correct, as I shall show. Filipjev (1927) considered the short mandibles and lack of onchia in *Enoplus* to be primitive while Chitwood (1950) appears to suggest that this condition is not primitive, an opinion which Wieser (1953) advances unequivocally. The mandibles appear to have been dismissed by all previous workers as relatively simple wholly homologous structures. Thus Wieser (1953 and 1959), for example, refers to rods or bars connected anteriorly by a curved bar and goes so far as to distinguish between two genera on the character that the mandibular pillars are rod-like in one and are plate like in the other (*Mesacanthion* and *Epacanthion*). In fact the mandibles are, in most cases, one curved mass of thickened, darkened cuticle developed in the cuticle lining the anterior end of the oesophagus and the buccal cavity. The apparent presence of rods, pillars, plates or similar elaborations is due in most cases to studying the incurved ends of these plates of dense cuticle in optical section. Thus the descriptions simply refer to the thickness of the modified cuticle making up the mandibles.

GENERAL MORPHOLOGY OF THE HEAD

It is essential to consider the head as a unit. To consider only one part in isolation must, inevitably, lead to error. Further, in all the other groups which I have

studied it has been possible to show that the structure of the head—that is the form of the mouth opening and bounding lips or lip-like structures, the shape of the buccal cavity and the modification of the anterior end of the oesophagus—forms a functional whole and must be analyzed as such (Inglis, 1958, 1960 ; Inglis & Diaz-Ungria, 1960). This is equally true in this group of nematodes. The most significant and probably the most immediate factor in determining the form of the head in the Enoplida is the way in which the oesophagus is attached to the outer body wall or the cuticle of the body. To this simple yet effective modification may be attributed part of the success of the Enoplida. This success is amply witnessed by the large size and numbers of the members of the group and their widespread occurrence in marine, fresh-water and soil habitats and as parasites. Their success is not wholly to be attributed to this since the appearance of spiral fibres within the cuticle must also have played a large part in their evolutionary advance (see Inglis, 1964). In fact the structure of the cuticle supplies one of the most conservative characters of the entire Order. Associated with the attachment of the oesophagus to the body wall over a large area at its anterior end is the modification of the inner layer(s) of the body cuticle to produce the spectacular *cephalic capsule* so characteristic of forms such as *Thoracostoma*. But the most unexpected result of the present study has been the realization that the mandibles of the Enoplidae are very closely associated with the distribution of the nerves which supply the inner circle of cephalic sense organs and that their functional origin must have been that of supporting structures, a function which they still clearly fulfil even in highly modified groups.

The head types fall into two major structural groups, one in which the oesophagus is attached at its anterior end to the outer body wall and a second in which there is no such attachment, or at least such an attachment is not obvious. The first group is frequently characterized by the presence of a dense component derived from the inner layers of the cuticle (endo- and meso-cuticle ; see Inglis, 1964) at the anterior end of the body, the *cephalic capsule*. In many genera this is the only obvious modification of the head. It frequently corresponds to the zone of attachment of the oesophagus to the body wall but not always and not wholly. It also tends to be more obvious in forms with well developed buccal armature (e.g. *Thoracostoma*). The cephalic capsule is frequently divided into lobes posteriorly by a series of *incisions* (see Wieser, 1954) of which, when they are present, there are always six, two lateral, two dorso-lateral and two ventro-lateral. Such incisions are always present when the cephalic sense organs lie anterior to the posterior edge of the cephalic capsule and represent the external expression of the internal foramina—between the body wall and the oesophagus—through which the nerves pass. The capsule is frequently roughly punctate and this appears to be a reflection of the fusion of the oesophagus to the body cuticle since such markings do not occur over the incisions. In most cases the incisions expand anteriorly to form roughly circular areas from which the cephalic setae arise. These are called *fenestrae*. In some cases the external covering of the anterior end of the oesophagus becomes thick and dense to form a second capsule, which I shall call the *oesophageal capsule*

(see Text-fig. 1). This is what Wieser (1954) calls the pharyngeal capsule but at that time he was calling the oesophagus the pharynx. This is technically correct, as Hyman (1951) points out, but the term oesophagus is so firmly embedded in nematode literature that to attempt to extract it would only lead to complications with no compensating advantages. Wieser (1954) proposes the term "stomadaeal capsule" for two subsidiary capsules—the oesophageal capsule and the "Buccal capsule" (my terminology) which he considers to be "... built up of the walls of the vestibulum, buccal cavity and the anterior pharyngeal lumen ...". I do not accept the term stomadaeal capsule as it covers structures which arise from too many and too diverse origins to be adequately covered by one term. Further, the two sub-capsules proposed by Wieser are totally different in origin and function as I shall demonstrate below. The oesophagus is attached to the body wall in the region of the cephalic capsule at three zones in some forms, e.g. *Enoplus*, over most of the length of the capsule while in others the attachment is complete round the

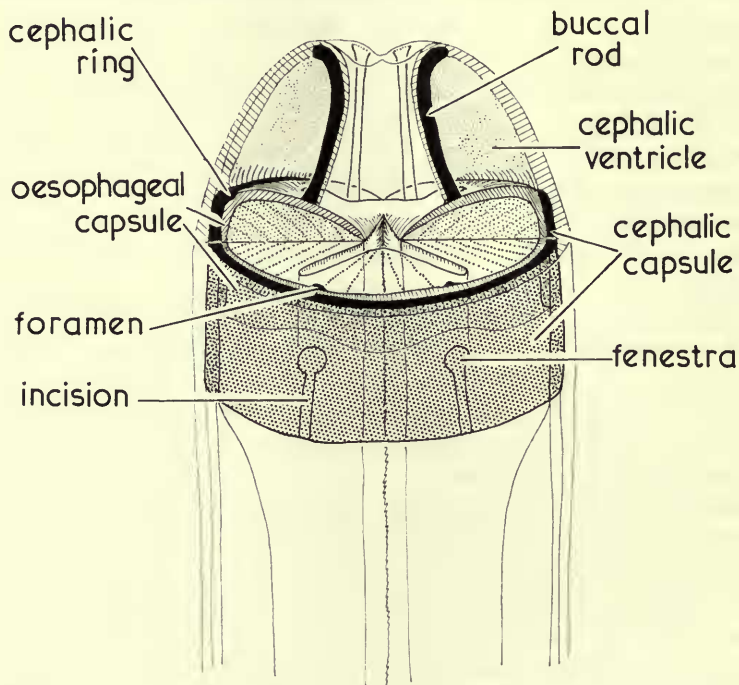


FIG. 1. Sectional view of a generalized Enoplida head from the dorsal surface.

circumference of the oesophagus for most of the length of the cephalic capsule, e.g. *Enoplolaimus*. In all cases the union between the oesophagus and the body wall is complete at the anterior end of the oesophagus, with the minor exception of the foramina through which pass the nerves to the inner circle of or *labial sense organs*. At this point of complete fusion or the level at which the oesophagus terminates anteriorly the cephalic capsule is frequently thickened as a distinct ring, the

cephalic ring. Wieser calls this structure the "stomadaeal ring" but its origin from the cephalic capsule is quite clear when the relationships to the nerves which supply the labial sense organs are studied. These nerves always pass beneath the cephalic ring, showing that the ring does not take its origin from the oesophagus (see Text-fig. 87). The oesophagus, in many of the elaborate forms, stops some distance posterior to the extreme anterior end of the body and it is in such forms that a prominent cephalic ring occurs. The remainder of the body anterior to the oesophagus is a fluid filled space (see Figs. 1 and 2) which is much reduced in some forms with complex cephalic armature, e.g. *Enoplus*, *Enoplolaimus* and *Thoracostoma*, but is prominent and obvious in forms such as *Dayellus* (Text-figs. 38 and 41). This is the space I propose to call the *cephalic ventricle* and it is this space which has led Filipjev to misinterpret the way in which the cuticle of the body is attached to the oesophagus. The occurrence and appearance of all these structures varies, for example the cephalic capsule extends anterior to the cephalic ring in some forms; in others there is no cephalic vesicle, and various other structures also occur. This variation in the occurrence and form of the morphological structures will be treated in detail below, by families.

THE STRUCTURE OF THE HEAD IN THE PHANODERMATIDAE

I have previously reported the presence of six cuticular rods, in the genus *Phanoderma*, which are developed within the cuticular lining of the buccal cavity (Inglis, 1962) and have found them in another species of the same genus, *Phanoderma unica* (see page 309). The same structures are present in *Dayellus dayi* (see page 304) where they are much more easily seen as the anterior end of the oesophagus in this genus is simple (Text-figs. 38 and 41). These rods, which I propose to call *buccal rods*¹ (Text-fig. 1), are always closely associated with the nerves which supply the labial sense organs (Text-figs. 38, 39, 41, 50, 53 and 54), (I shall use the term *buccal cavity* to mean the lumen of the digestive tract from the anterior end of the oesophageal lumen to the exterior.). In *Dayellus* the cephalic and oesophageal capsules are fairly well developed, the cephalic ventricle is very prominent and the anterior end of the oesophagus is simple without armature of any kind. That is, there are no onchia, plates or other elaborations of any kind (Text-figs. 38 and 41). The mouth opening is bounded by six lobes and there are no flaps by which it can be closed (Text-fig. 39). The genus *Phanoderma* is as described before (Inglis, 1962) with well developed cephalic and oesophageal capsules, two massive cuticular *onchia* ventrally and one small *onchium* dorsally (*Onchium* is a name proposed by Cobb (1919) for tooth-like structures which arise from the oesophagus and *odontium* applies to similar structures arising from the lining of the buccal cavity). Six buccal rods are present and the mouth opening is bounded by six lip-lobes as in *Dayellus*. A cephalic ventricle is present but is reduced relative to the condition in *Dayellus* (Text-figs. 50, 53 and 54. Figs. 7-9 and 12-13 in Inglis, 1962). It should be noted that in *Phanoderma* the onchia project freely into the buccal cavity and are not embedded in the walls of that cavity. In some species of *Phanoderma* the

¹ Definitions of all the morphological terms proposed or employed are given on p. 296.

body cuticle posterior to the cephalic capsule is marked by longitudinal striations which form the so-called *cervical capsule*. Such a capsule is not present in *P. unica* but is present in, for example, *P. parafilipjevi* which I redescribed in 1962.

Two species of the genus *Crenopharynx* are described later (pages 306 and 308) and the structure of the head is the same in both. The cephalic capsule is lightly built and there does not appear to be an oesophageal capsule. The cephalic ventricle is slight and no buccal rods appear to be present when the head is studied in any view other than *en face* (Text-figs. 43 and 49). The anterior end of the oesophagus is covered by fairly thick cuticle (?incipient oesophageal capsule) and projects anteriorly as three lobes. These lobes appear to project freely into the buccal cavity and do not lie embedded in the surrounding cuticle of the buccal cavity. I cannot, in view of the small size of the specimens, be sure but in *en face* preparations the cuticle covering the radial surfaces of the anterior lobes of the oesophagus appears to be in two layers, one from the oesophagus and one from the wall of the buccal cavity. The mouth opening is tri-lobed and in surface view, *en face*, the inner circle of sense organs appears to be supported by a series of buccal rods (Text-fig. 43). A more careful examination, however, shows that this effect is due to a thickening of the cuticle lining the buccal cavity. Because the oesophagus is developed anteriorly as three lobes each lobe projects between a pair of the nerves supplying the inner circle of sense organs. Also, each arm of the lumen of the oesophagus, or buccal cavity, lies between a pair of these nerves so that each nerve is separated from one neighbour by a lobe from the oesophagus and from the other neighbour by one of the radii of the buccal cavity. As a result each nerve, and as a corollary each labial papilla, is enclosed in a V-shaped cuticular structure one arm of which corresponds to one side of the radial lumen of the buccal cavity and the other arm of which corresponds to one side of a lobe of the oesophagus (see Text-figs. 43 and 44). This arrangement of the head and its contained structures reflects the mechanical necessity of fitting twelve structures into the circumference of the body, the three radii of the oesophageal/buccal cavity lumen, the three anterior lobes of the oesophagus and the six nerves to the labial sense organs. It will be argued later that this condition could represent the origins of the buccal rods occurring in forms such as *Phanoderma* and *Dayellus*.

Throughout this family the labial sense organs appear as papillae while the outer or *cephalic sense organs* are in the form of setae and always lie in one circle of ten of which six are longer than the remaining four. The extent to which the oesophagus fuses to the outer surface of the body is difficult to establish in view of the relatively small size of the head in all members of the family but it appears to take the form of three zones of attachment which widen anteriorly until the fusion is complete near the posterior end of the cephalic vesicle, when present. There are no marked modifications of the cephalic capsule in the form of incisions or fenestrae.

THE STRUCTURE OF THE HEAD IN THE ENOPLIDAE

The form of head characteristic of this family is the most complex in the entire Order and is the form which I have been able to study most thoroughly. Its

structure will be considered under two headings, the skeletal component and the muscular. It should be noted that in this family, in particular, all the dense cuticular components are developed within the thickness of the cuticle, and, apparently, always in the deepest layer(s) (see Inglis (1964) for a detailed discussion). As a result the mandibles which are so prominent and so important taxonomically lie within the sheets of cuticle forming the walls of the buccal cavity and simply represent specializations of these sheets and not independent organ systems. The labial sense organs take the form of an inner circle of setae in all the genera, except *Enoplus*, and the cephalic sense organs occur in roughly one circle of setae of which six are longer than the remaining four. In many cases, however, this arrangement becomes more condensed so that each of the four short setae lies immediately posterior to the dorso- and ventro-lateral representatives of the six long setae (see Text-figs. 29, 30, 55, 59, 60, 62, 74, 76, 86, 87, 91, 98, 104 and 109). In addition to the setae there are the usual lateral amphids, which are generally small and lie about the posterior edge of the cephalic capsule, and a pair of sense organs which are latero-ventral in position between the two circles of sense organs. These *cephalic slits* appear to be universal among the members of the Enoplidae and show marked variation from genus to genus. They are small in some, such as *Enoplus*, and very large in others, e.g. *Mesacanthion* (Text-figs. 77, 79 and 85) and *Trileptium* (Text-figs. 99 and 100), but in all such cases the organ consists of a small opening to the exterior which leads in to a chamber of varying size from the base of which a nerve runs posteriorly and the difference in the appearance from species to species is determined almost wholly by the size and shape of this chamber. In a few cases the cephalic slit is modified to form what Wieser (1953) has called a *cirrus*. This is a long anteriorly projecting club-shaped organ which arises from the same position as that generally occupied by the cephalic slit and is clearly a modification of that organ. Wieser (1953) reports it from three species, *Oxyonchus dentatus* Ditlevsen, 1919, *Parasaveljevia lupata* Wieser, 1953 and *P. cirrifera* Wieser, 1953. Later (1959) from *Oxyonchus culcitatus* Wieser, 1959, he reports a well-developed cirrus in the same region of the head and in an *Oxyonchus* species he describes a slight elevation. A well developed cirrus is present in *O. ditlevseni* (page 311, Text-fig. 57). As Filipjev (1927) suggests, in the case of the small elevations he has seen, these cirri are possibly due to the eversion of the pocket of the cephalic slit. The small inner pocket of the cephalic slit in *Enoplus* looks suspiciously like an introvert cirrus, or vice versa.

SKELETAL COMPONENT OF THE ENOPLIDAE HEAD

A cephalic capsule is always present and well developed and there are always three *mandibles* of varying shape and degrees of massiveness present, one corresponding to each sector of the oesophagus. A distinct cephalic ring is always present and the anterior end of the oesophagus is always covered by thick cuticle to form a simple oesophageal capsule which does not appear to extend posteriorly much beyond the level of the cephalic ring. Posterior to the cephalic capsule in several genera there is a zone covered by dot-like markings. This appears to be homologous

with the cervical capsule of the Phanodermatidae. The cephalic ring persists round the entire circumference of the body (see Text-figs. 62, 76, 86 and 87) and tends to curve posteriorly in the inter-labial regions. The anterior surface of the oesophagus always slopes posteriorly from the level of the cephalic ring towards the interior of the body so that its attachment to the complex of internal cuticular structures is always at a level more posterior than its outer limit (Text-figs. 16, 17, 24, 34, 57, 60, 62, 70, 74, 80, 100, 104 and 110). The mouth opening is tri-radiate with three large lips which are separate for some distance posteriorly along the body.

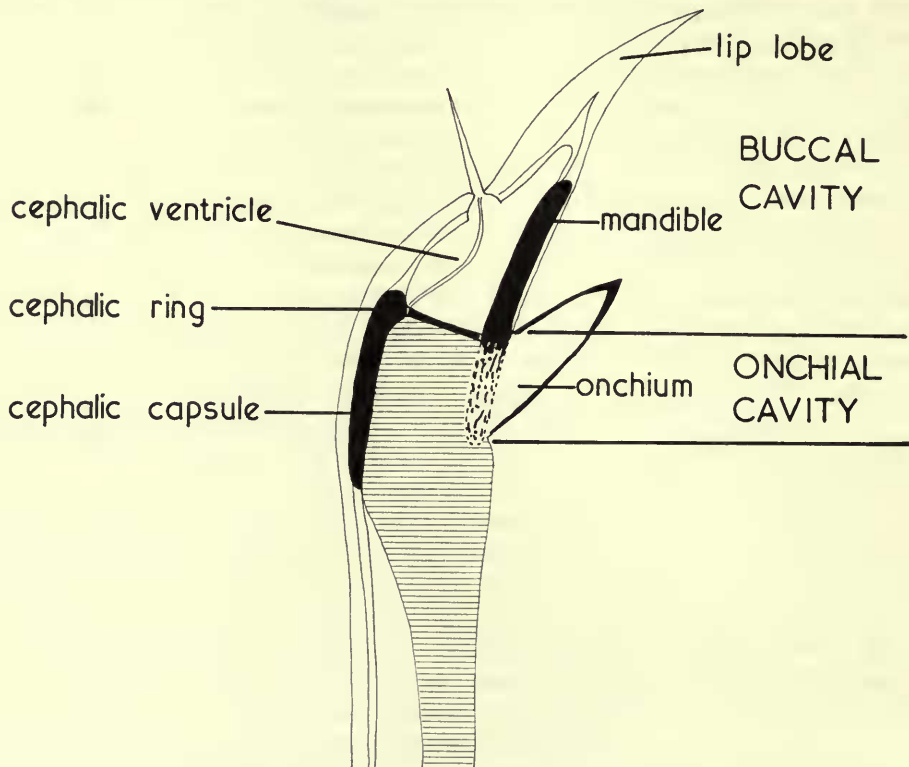


FIG. 2. Generalized longitudinal section through one lip of an Enoplidae head.

In effect the mouth opening is three dimensional in comparison to the terminal condition occurring in the Phanodermatidae which can be described as two-dimensional (see Inglis (1962) where I employ the same terms in the same way). The cuticle on the inner face of each lip is thickened over a specialized median zone to form the dense mandibles and the cephalic ventricle is subdivided by the posterior extension of the mouth opening to form three subsidiary pockets, one corresponding to each lip, each of which, in turn, corresponds to one sector of the oesophagus. The anterior limit of each ventricle is just anterior to the anterior edge of the corresponding mandible. Anterior to this line of fusion the lip is a solid sheet of cuticle which I shall call the *lip-lobe*. This lip-lobe thins evenly towards its rounded

anterior edge which is developed in most cases into a small subsidiary lobe (Text-figs. 59, 60, 70, 85, 86 and 90). The lip-lobe is generally thickened on each edge along a zone corresponding to the edges of the mandibles (Text-figs. 85, 90, 93 and 95).

The most typical condition in this family is for the anterior end of the oesophagus to be cupped to form a cavity into which project three massive wholly cuticular onchia. Thus the entire mouth cavity is derived from two sources and is divided into two parts, one lying anterior to the anterior end of the oesophagus on a level corresponding with that of the cephalic vesicles and one lying posterior to the anterior limit of the oesophagus, which is wholly surrounded by oesophageal tissue or specializations of oesophageal origin, in which lie the onchia. The first of these chambers I shall call the *buccal cavity* and the second the *onchial cavity*. Thus, if a lip is considered in longitudinal section through its mid-line there are four points of reference, one—the point of fusion where the ventricle stops anteriorly, two—the anterior edge of the mandible, three—the anterior end of the oesophagus and four—the posterior end of the cephalic capsule (Fig. 2). The two cavities show some variation in shape. The onchia may be equal in size, as in *Enoploides* or *Mesacanthion*, or the dorsal may be much smaller than the two equal ventro-lateral as in *Oxyonchus* (Text-fig. 55). Except in some very exceptional genera, e.g. *Trileptium*, no other variation is shown by the onchia except for a gross variation in their size and their complete reduction in *Enoplus*. The cuticle lining the onchial cavity is always thickened but the degree of this thickening varies considerably. For example it is not marked in forms such as *Africanthion* (Text-figs. 91 and 95) but is very marked in forms such as *Mesacanthion* (Text-figs. 84 and 89).

The mandibles are generally described as consisting of two lateral pillars with an anterior, curved connecting bar, except in a few special cases such as, for example, *Hyalocanthion* Wieser, 1959. This is incorrect, although a reasonable description of the appearance of the mandibles from a superficial examination. In all the forms I have studied the mandibles represent a solid thickening of the lining of the buccal cavity wall which curves with the shape of the body so that, when it is viewed from the outer aspect there appear to be two bars because the mandible is being studied in optical section. Thus Wieser's (1953) separation of the genera *Epacanthion* and *Mesacanthion* on the presence of rod-like or plate-like lateral pieces to the mandibles is based on a misunderstanding of the conditions present. This does not invalidate the use of such characters since it may still be valuable to use the thickness of the mandible in this way. When the inner surface of the lip is studied a distinctly striated semi-circular zone of cuticle is seen flanking the mandibles which I propose to call the *semi-lunar striations*. (Text-figs. 30, 36, 61, 72, 95 and 101). The more anterior limit of this striated area runs from the tip of the mandible and curves round to the inter-labial spaces and terminates along a posteriorly curved line posteriorly. This posterior limit lies at the level of the anterior edge of the oesophagus where it attaches to the onchial cavity. The mandibles project from the surface as two small points or processes at their extreme antero-lateral tips only (Text-figs. 61, 89 and 95). Posteriorly the mandibles narrow and then flare out again to form part of a transverse bar of dense cuticle which extends from one

flanking inter-labial space to the other. It is along this bar that the semi-lunar striations stop posteriorly. Immediately posterior to this bar, which I propose to call the *mandibular ring*, is the line of attachment of the oesophageal tissues to the thickened cuticle lining the onchial cavity. The separation between the two cuticular masses at this level is shown clearly in forms such as *Enoploides* (Text-fig. 30) but in extreme cases, such as *Mesacanthion*, the mandibles become so closely associated with the cuticle of the onchial cavity—the *onchial plate* as I shall call it—that there appears to be only one structure present. Similarly in *Enoplus*, in particular, the fusion of the buccal and onchial components has been carried so far

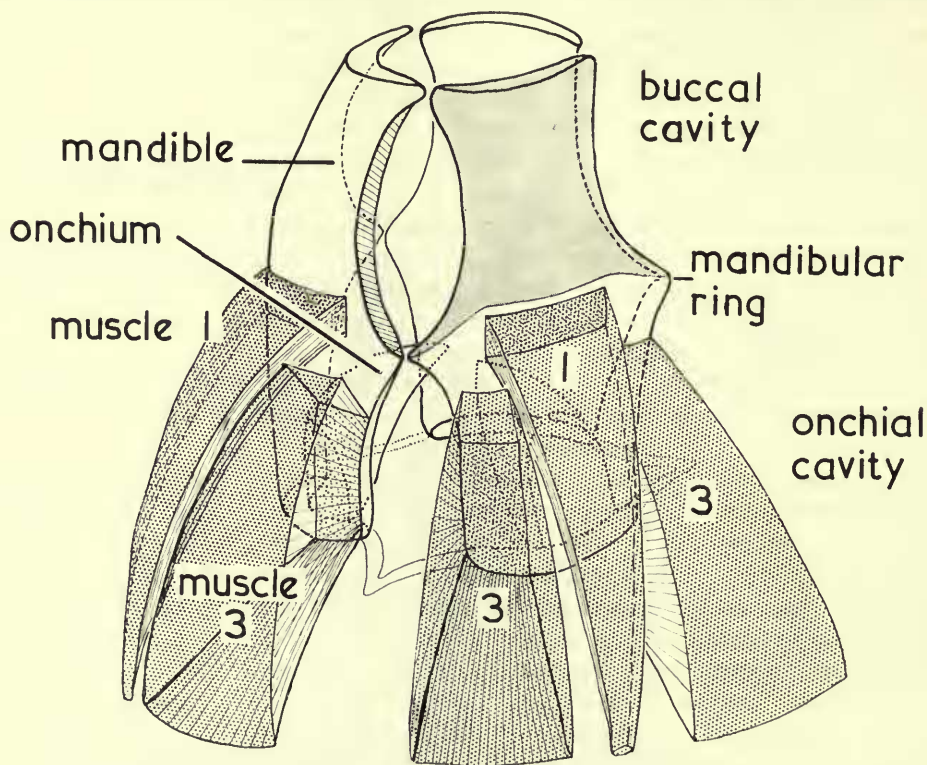


FIG. 3. The mandibular : onchial complex of a generalized Enopliidae head with simplified musculature.

that there is only one functional and, apparently, morphological unit left. Nevertheless even here the division into an anterior and a posterior component can still be made out and over the entire family it is clear that the term mandible has been applied in different ways in different genera. In *Enoplus* the whole complex is what has been called the mandible while in *Enoploides*, for example, what have been called mandibles are really only the buccal component of the entire complex. This latter use of the term has, in general, been the more common and I therefore restrict its use here to that sense. The *mandibles*, therefore, represent a thick dense specialization of the median part of the cuticle lining the buccal cavity.

In all cases the mandibles and the onchial plates form a functional unit which is broad antero-posteriorly in its middle region but narrows rapidly towards the edges of the lips—that is towards the inter-labial spaces—so that the onchial plate forms a massive central plate, which corresponds to each oesophageal sector, supported by two processes, the *radial processes* (Text-figs. 5–7) which extend laterally to meet at the outer ends of the oesophageal radii (Text-figs. 69, 83 and 87). It should be noted that the mouth opening is closed radially by external cuticle much further

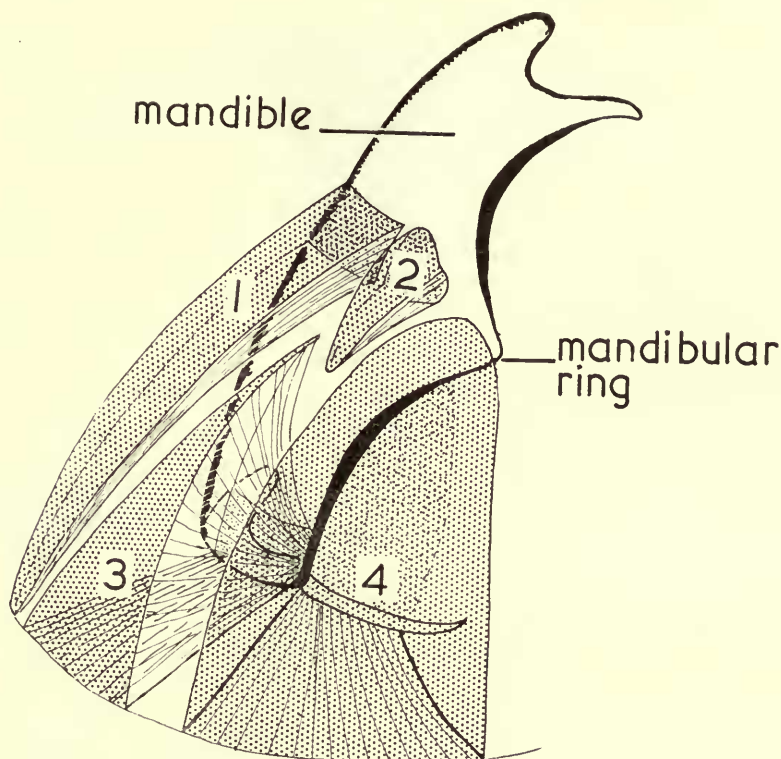


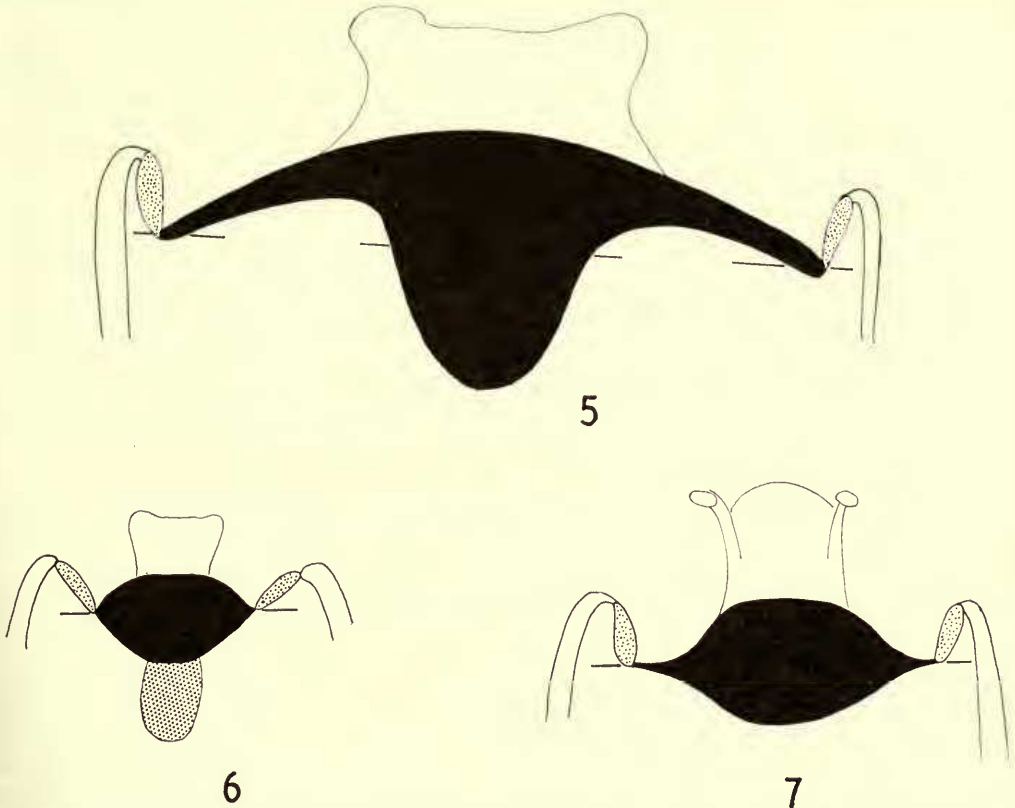
FIG. 4. The mandibular : onchial complex of one lip of a generalized Enoplidae head with complete musculature. The numbers refer to the musculature as numbered in the text on page 283.

anteriorly than it is internally (Text-figs. 62, 76, 80 and 87). Internally the separation of the lips and the sectors of the onchial cavity continues to the level of the mandibular ring—which effectively forms the anterior limit of the onchial plate. The musculature at the anterior end of the oesophagus is highly specialized (see page 283) and from about the level of the posterior edge of the cephalic capsule forward the parts of the oesophagus opposite the outer ends of the radii of the oesophageal lumen become increasingly cuticularized. These zones of dense material lying within the oesophagus I shall call *radial masses* (Text-figs. 5, 6, 7, 25, 26, 29 and 80) and the onchial plates are attached to these masses by their radial

processes. The onchial plate, therefore, represents a specialized, thickened zone of cuticle, which is slung from the radial masses (Text-figs. 5, 6, 7 and 29). The mandibular ring and the associated parts of the anterior edge of the onchial plate curve posteriorly as they pass radially towards the radial masses. Thus the points at which the plates and radial masses fuse are always posterior to the level of the cephalic ring, and generally lie on a level which is just anterior to the anterior origins of the onchia (Text-figs. 5, 6 and 7). The functional significance of this is discussed below (page 285).

In *en face* view the mandibles are curved to correspond to the curvature of the buccal cavity and the nerves which supply the labial sense organs always lie in the same relationship to them. That is, the nerves run anteriorly along a line running antero-posteriorly behind the dorso- and ventro-lateral components of the cephalic sense organs. Just posterior to these setae the nerves curve towards the interlabial spaces and run to the labial sense organs along the line of, and in close association with the edges of the mandibles (see Text-figs. 30, 31, 72, 74, 79, 84, 87 and 91). This arrangement is absolutely constant no matter how the mandibles may be modified. The mandibles, themselves, appear to arise from two distinct sources, from a thickening of the wall of the buccal cavity to form a large median plate which is flanked by rods of thickened cuticle which are associated with the nerves supplying the anterior sense organs. This is most clear in *Enoplolaimus mus* (Text-figs. 60, 61, 68 and 72) and *Oxyonchus dittevseni* (Text-figs. 55 and 59) in which the mandibles are not as fully fused to the onchial plates as they are, for example, in *Mesacanthion* (Text-figs. 79 and 84) although even in this latter genus a *mandibular rod* component can be identified. In *Enoplolaimus mus* the mandibles, when viewed from the external or internal surface of the lip, arise from the level of the mandibular ring as a thickening of the cuticle on the mid-line of the lip (Text-fig. 61). More anteriorly two flanking rods separate from the central mass, the *mandibular plate*, and these two rods curve inwards and become pointed as the claws of the mandibles (Text-figs. 61 and 72). This is even clearer in *en face* view (Text-figs. 63, 64, 65, 66 and 67) where it can be seen that the mandibular plate not only curves circumferentially, independent of the mandibular rods, but also curves inwards anteriorly so that the plate forms a cup-like recess in the inner surface of the lip. In forms such as *Mesacanthion* the rod component is not so distinctly separate and has become incorporated into the main mass of the mandible except at its anterior end (Text-figs. 79 and 84) while in *Africanthion* no trace of a rod element is present (Text-figs. 91, 95 and 98). No distinct rod element can be seen in the mandibles of *Trileptium ayum* (Text-figs. 100 and 101) nor in *Thoracostomopsis carolae* (Text-figs. 104 and 107), but in the latter genus this could be over-looked because of the very small size of the head. Finally, when the head is considered in *en face* view, the cross sectional shape of the buccal and onchial cavities varies from one level to another. In general the buccal cavity is circular in transverse section at its anterior end but extends along the lines of the radii until at the level of the mandibular ring it is roughly triangular in section. Posterior to this ring the onchial cavity is triangular in section and the oesophageal sectors, from the anterior

ends of which the onchia arise, slowly extend inwards until the typical tri-radiate condition of the oesophageal lumen is wholly established. The most important result of this alteration in the shape of the combined cavities is that the onchial plates, the mandibular ring and the radial processes tend to form a straight line in transverse section.



FIGS. 5-7. Outlines of the mandibular : onchial-plate : radial mass complex in *Mesacanthion studiosa* (Fig. 5), *Enoplus harlockae* (Fig. 6) and *Enoplolaimus mus*. Note the backward sweep of the mandibular ring and radial processes and the level at which they are attached to the radial masses.

The degree of development of these various skeletal components of the head varies from genus to genus and the detailed structure in each of the genera I have studied is as follows:

Enoplolaimus: the cephalic capsule is rather short and the outer circle of cephalic setae arises from about midway between its anterior and posterior limits (Text-figs. 60 and 62). The onchia are small and lie mainly posterior to the mandibular ring. The onchial plates are poorly developed and the radial pieces are small. The onchial cavity is deep and narrow and gives the appearance (Text-fig. 60) referred to by Wieser (1953) and Mawson (1958), in some species of the genus *Mesacanthion*, as

pocketed. Whether this is a constant character or is a functional distortion I do not know but all the specimens of *E. mus* have this appearance. It should be noted that this "pocketing" is due to the radii of the onchial cavity seen in optical section and reflects the fact that the sectors of the oesophagus are narrow at this level. The cephalic ring is well developed and the head anterior to it is short and stout (Text-figs. 60 and 62). The mandibles are not wholly fused so that all the component parts—the mandibular rods and mandibular plate—can be seen. There are two large, squarish cuticular thickenings developed in the cuticle covering the *outer* surface of the head which appear to function as supports for the rather massive labial setae (Text-figs. 62, 67 and 72). The inner surfaces of the lips carry semi-lunar striations (Text-figs. 61 and 72).

Africanthion: the mandibles are lightly built with no indication of mandibular rods (Text-figs. 91, 95 and 98). The onchia lie wholly posterior to the mandibular ring and the lips are high and narrow. The dorsal onchium is slightly smaller than the two equal ventro-lateral and the cephalic capsule is short with the outer cephalic setae arising from its mid-level (Text-figs. 91 and 98). In optical section the edges of the mandibles appear as thin, light rods (Text-figs. 91, 95 and 98). The inner surface of the lips carries semi-lunar striations and the cephalic slit is small. The radial pieces are well developed.

Mesacanthion: the cephalic capsule is prominent with distinct granulations, forming a kind of cervical capsule, in the cuticle posterior to it (Text-figs. 74, 80 and 86). The outer cephalic setae arise from near the cephalic ring (Text-figs. 74, 76, 80, 84, 86 and 87). The mandibles are short, broad and massive, almost completely fused. The mandibular rods appear to be represented by two small cuticular lobes on the outer edges of the mandibles (Text-figs. 79, 80 and 84). The onchia are small and equal and lie wholly posterior to the cephalic ring. The onchial plates are very closely integrated with the mandibles so that there appears to be only one massive cuticular structure present with very distinct radial processes (Text-figs. 74, 84 and 89). The radial pieces are well developed. The mandibular/onchial plate complex is pierced by holes of undifferentiated cuticle so that they have a rough, unfinished appearance (Text-figs. 74 and 84).

Trileptium: the cephalic capsule is lightly built and the outer cephalic setae arise from its posterior edge (Text-fig. 101). The onchial cavity is large and the equal onchia extend anteriorly almost to the anterior limits of the mandibles within which they largely lie. The mandibles are small and compact, showing no indication of any component parts. They appear to act as an enclosing frame for the onchia (Text-fig. 101) which they enfold very closely when the head is viewed from the outer surface. The lips bear semi-lunar striations on the inner surface. The lumen of the mandibular cavity is tri-radiate in transverse section (Text-fig. 99) and not large and triangular as in most of the other head forms.

Oxyonchus: the cephalic capsule is fairly short and the cephalic setae arise from near the cephalic ring (Text-fig. 55). The ventro-lateral onchia are large and extend

anteriorly beyond the cephalic ring while the dorsal onchium is short and does not extend so far anteriorly (Text-figs. 55, 57 and 59). The mandibular rods are very distinct and the long, transversely narrow mandibular plate bears a series of small denticles arranged in two to three rows. Any definite description of these structures as being in two or three rows is not possible as their arrangement is not regular. The cephalic slits are represented by cirri (Text-figs. 57 and 59). The inner surface of the buccal cavity is marked by semi-lunar striations and large square thickenings of the outer cuticle of head are associated with the labial setae, as in *Enoplolaimus* (Text-fig. 59).

Thoracostomopsis : the structure of the head in this genus has been misinterpreted in the past. Ditlevsen (1919) and Filipjev (1927) both refer to the difficulty they had in analyzing the structure of the head and this I can well understand since it is very easy to make the error of describing a spear—as both these authors do—in the buccal cavity when studying the specimens from the side. However, when an *en face* preparation is studied the presence of three long structures in the mouth cavity is quite clear. In view of the other great similarities between the specimens I have studied and the descriptions given by both Ditlevsen and Filipjev I have no doubt that the conditions I found are also present in the species described by these authors. The cephalic capsule and ring are very distinct and the capsule is very strongly divided on its posterior edge to form six rounded lobes (Text-figs. 103 and 109) of which the dorsal and ventral are larger than the paired laterals. Filipjev (1927) describes three “. . . plaques indépendantes, correspondantes aux trois secteurs oesophagiens.” in *T. galeata* Filipjev, 1927 ; describes the capsule in *T. ditlevseni* Filipjev, 1927 as poorly developed and reports his inability to make out the details of the structure of the capsule in *T. longissima* Filipjev, 1927. Ditlevsen (1919), however, shows a capsule which is almost identical with that figured here. Filipjev (1934), in spite of his own and Ditleven's descriptions, describes the capsule in this genus as four-lobed, this is clearly an error. The head, anterior to the cephalic ring, is long and narrow and, as a concomitant, the cephalic ventricles are also long and narrow. The mandibles are also long and narrow with no apparent trace of their component parts. This is difficult to establish definitely because of the small size of the anterior part of the body. The cephalic setae arise about half way up the cephalic capsule (Text-figs. 103, 104 and 109). The onchia are very long, thin and sheet-like. The anterior part of the oesophagus is modified as a distinctly swollen region (Text-figs. 103 and 104) from which the modified onchia arise. The onchia extend anteriorly to about the anterior ends of the mandibles and, although they merge slowly into the oesophagus over the entire length of the anterior modification, their anterior line of origin is clear (Text-fig. 104). In *en face* view the onchia are seen to fold round each other to form a tube (Text-figs. 105 and 106). In the specimen studied *en face* the arrangement is as shown in Text-fig. 106 with the dorsal onchium enfolding the two ventro-lateral which in their turn overlap so that a distinct tube is formed. The head in this genus is, therefore, made up of the same components as all the other, more typical, members of the Enoplidae.

Enoploides : I have been able to study only one larval specimen of this genus and it shows the following combination of structures. The cephalic capsule is lightly built and all the sense organs are setose. The lips are large with terminal lobes and are marked internally by fine semi-lunar striations. These striations, as is usual, stop along a curved line originating at the slightly protruding tips of the mandibles (Text-fig. 30) and the outer edges of the lips beyond this line, are further marked by striations which are much further apart than the semi-lunars. The mandibles are narrow and solid looking. The onchia are small and arise from a somewhat thickened onchial plate. The division between the onchial and mandibular components of the mouth armature is clear (Text-fig. 30). The radial pieces are well developed (Text-fig. 29) and the cephalic ventricle is somewhat reduced. There is a supporting piece developed in the outer cuticular covering of the head which is associated with the mandibles (Text-figs. 29 and 30). There is no obvious cephalic ring.

Rhabdodemania : this genus is considered here for convenience (see discussion later, page 322). As Wieser (1959) suggests, the "cuticular projections" and the "three pairs of longer onchia" usually described for this genus may be interpreted as homologous with the onchia and mandibles, respectively, found in more typical Enoplidae. An *en face* preparation established this beyond doubt (Text-fig. 116). In the species I describe later (*R. nancyae*, page 322) the mouth opening appears to be large and circular but it is difficult to be sure as the specimens are in a somewhat poor condition, but the lining of the mouth opening is striated. Wieser (1959) refers to "... strongly developed, cushion-like lips" but he is clearly referring to the stout, projecting anterior end of the body (Text-fig. 117). A very poorly developed cephalic capsule may be present but once again I cannot be sure. Nevertheless the cuticle at the anterior end of the body is very thick and the oesophagus is fused to it for some distance back from the anterior end (Text-figs. 117 and 121). I would interpret the outer striated part of the mouth cavity as being homologous with the buccal cavity of more typical forms. The next part, that is the thick cuticle lying anterior to the end of the oesophageal musculature and posterior to the striated capsule, I interpret as the highly modified mandibles while the cavity posterior to this (in which in my species there is a large dorsal and two very small ventro-lateral onchia) as the onchial cavity. The labial sense organs are papillae and the cephalic are setae in one circle.

Enoplus : the cephalic capsule is short and without incisions or fenestrae. The cephalic setae are short and stout in one circle and the labial sense organs are papillate. The cephalic ventricle is almost completely reduced in association with the loss of onchia and the onchial cavity and the general shortening of the mandibles and lips. The cephalic ring is very prominent. The mandibles are narrow and, in association with the onchial plate, appear to form one massive, dense median structure at the anterior end of each sector of the oesophagus (Text-fig. 110). The entire inner surface of the buccal cavity appears to be striated as in *Enoploides* and the oesophagus is fused to the cephalic capsule along three zones which correspond

to the three sectors of the oesophagus over most of the length of the capsule (see Inglis, 1962). The lumen of the buccal cavity is tri-radiate. The whole head, in fact, represents a condensation of the components present in the other members of the family with a great reduction of all the cavities and structures. It should be noted that the onchial plate can still be distinguished from the mandibles (Text-fig. 31).

MUSCULAR COMPONENT OF THE ENOPLIDAE HEAD

The anterior end of the oesophagus is modified into a number of distinct muscles which are attached mainly to the onchial plates. All the muscles are the result of specialization of that part of the oesophagus which corresponds to the cephalic capsule and are arranged in two transverse rings within the anterior part of the oesophagus. They are arranged in the same way in all the three sectors of the oesophagus so that the description of the set corresponding to one sector of the oesophagus applies to all three. All the muscles are inserted on the onchial area, none are inserted on the mandibles, no muscles originate from outside the oesophagus and all the muscles have their origins on the outer surface of the oesophagus. The arrangement of these muscles is very constant throughout the various species I have studied. I have been unable to find any previous record of the form and distribution of these muscular specializations so that I can only discuss the range of modification in the species I have seen. The arrangement of the muscles is most easily understood from text-figs. 3 and 4. In each sector of the oesophagus there are three muscles in the anterior ring and four muscles in the more posterior. The origins of the more anterior muscles extend posteriorly to pass between the origins of the components of the more posterior ring (Text-figs. 4, 13, 20, 23, 28 and 33). These muscles will be discussed under numbers, thus: MUSCLE-1 is the median, unpaired muscle of the anterior ring, MUSCLE-2 occurs as a pair of muscles of the anterior ring, one on each side of Muscle-1. MUSCLE-3 occurs as a median pair in the more posterior ring and they are separated from each other by the tail of the origin of Muscle-1. Flanking Muscles-3 is a further pair, MUSCLE-4, which are sometimes very difficult to locate in dorsal or ventro-lateral view and are sometimes partly separated from Muscles-3 by the tails of the insertions of Muscles-2. (Text-figs. 13 and 20). The muscles of the anterior ring, Muscles-1 and -2, run anteriorly and inwards to insert on the onchial plate just posterior to the mandibular ring. They are thin posteriorly and become increasingly stouter and broader anteriorly. Muscles-2 are always smaller and shorter than Muscles-1. Muscles-3 insert on the posterior part of the onchial plate and are the most massive component of the musculature (Text-figs. 13, 20, 23 and 28). They are, in longitudinal section, somewhat fan-shaped running inwards to insert over a rather small posterior area of the onchial plate (Text-figs. 14, 17, 19, 25, 27 and 32). Muscles-4 insert on the thinner cuticle which flanks the onchial plate and lines the more radial parts of the onchial cavity (Text-figs. 4, 10, 12, 14, 15, 19, 25, 27 and 32). Posterior to these specialized muscles the oesophageal musculature runs wholly radially but is divided into two blocks in each sector by the lumen of the duct of the oesophageal gland (Text-figs. 9 and 35). Muscles-3 and -4 first appear at about the level at which the gland ducts narrow to form the relatively fine terminal portion. The lumen

of the oesophagus expands very quickly at the same level, to form the onchial cavity, by the disappearance of the axial parts of each of the oesophageal sectors (Text-figs. 9 and 27). Thus, in longitudinal section the onchial cavity appears as a step in the outline of each oesophageal sector. The transition from the wholly radial arrangement of the muscles to the two rings of specialized muscles is fairly abrupt with no obvious zone of transition. As the oesophageal duct narrows the sheets of muscle flanking it extend slightly and then the specialized musculature begins. In transverse section the foramina through which pass the nerves to the cephalic sense organs always lie between Muscles-3 and -4 (Text-figs. 12 and 25). The general arrangement of the muscles, with their directions of action is shown in Text-figs. 3 and 4. This arrangement is present in all the species I have studied although there is some variation co-related with the degree of fusion or development of the various skeletal components of the head. Thus, in *Mesacanthion* (Text-figs. 9-17) all the muscles are very prominent with a slight suggestion that Muscles-4 are divided into two parts. This appears to be due to the foramina through which pass the nerves supplying the labial sense organs (Text-fig. 11). In *Enoplolaimus* the Muscles-1 and -2 appear to be much more closely packed together anteriorly, associated with the much narrower anterior edge to the onchial plate; this is, in its turn, associated with the narrow mandibles (Text-fig. 20). Also in transverse sections, Muscles-3 and -4 are rather slim and lie far apart (Text-fig. 19). In *Africanthion*, although all the muscles are clearly present, because of the poor condition of the specimens I have been unable to establish the exact arrangements of Muscles-2 so that the conditions shown in Text-fig. 23 are only approximate. However, as is clear from Text-figs. 24 and 25, as far as it is possible to establish, the musculature is the same in principle as that previously described. The radial masses are very well developed (Text-fig. 25) and Muscles-4 are relatively massive in comparison to Muscles-3 while the musculature of the oesophagus surrounding the anterior part of the gland duct is very lightly developed (Text-fig. 25). In *Trileptium* the same arrangement of muscles occurs with the major difference that Muscles-4 stop relatively far posteriorly, probably in association with the great development of the radial masses. In this form the oesophagus is attached to the cephalic capsule along three zones for a large part of the cephalic region. In *Enoploides* Muscles-1 and -2 appear to fuse anteriorly to form one sheet and Muscles-3 are separated by the tails of all the muscles of the anterior ring (Text-fig. 28). That is, the posterior parts of the origins of Muscles-2 lie between the origins of Muscles-1 and -3 instead of between Muscles-3 and -4 as in, for example, *Mesacanthion*. Finally in *Enoplus* Muscles-1 and -2 are completely fused, except for a possible slight indication of a division near the anterior edge in some specimens (Text-fig. 33), to form one muscle mass which is flanked by long, narrow Muscles-3 which in their turn are flanked by Muscles-4. The general arrangement of the muscles, is however, the same as in all the other groups. That is, the large anterior muscle, Muscle-1/2 sheet, is inserted on the onchial plate just posterior to the mandibular ring while Muscles-3 are inserted at the posterior edge of the onchial plate and Muscles-4 are inserted on the lining of the oesophagus bordering the onchial plate.

FUNCTIONAL ANALYSIS OF THE ENOPLIDAE HEAD

The complex structures found in the head in the family Enoplidae are all functionally interrelated. The most obvious morphological feature of the head is the massive mandible : onchium system which must function as a unit although the component parts are derived from different sources. All the muscles are attached to this complex posterior to the mandibular ring which represents the posterior limit of the mandibular component of the complex. Thus the Muscles-1 and Muscles-2 will act so as to pull the mandibles outwards and backwards while causing the onchia and onchial plates to move inwards and forwards. Muscles-3 will act in apposition to these and on contraction reverse the movement, pulling the onchia and onchial plates posteriorly and outwards while causing the mandibles to move inwards and posteriorly (Text-fig. 8). The role of Muscles-4 in this is not clear. They do not appear to be essential, in view of their great reduction in *Trileptium*, but might act simply to re-inforce Muscles-3. It appears more probably, however, that Muscles-4 simply act to dilate the lumen of the oesophagus near its anterior end and so may be considered to correspond in action to the unspecialized oesophageal musculature found more posteriorly. The onchial plate is the development of the inner cuticle at the anterior end of the oesophagus on which the specialized muscles, 1, 2 and 3, have their insertions while the cephalic capsule corresponds to the part of the oesophagus from which they have their origin. The most immediate question is, round what point do the complexes rotate? At first it is difficult to see how such a system can rotate under the action of the muscles. However, when the form of the onchial plate is studied, most easily in specimens under pressure, it is not a symmetrical structure but is curved posteriorly along its anterior edge. Thus the radial processes are directed slightly posteriorly (Text-figs. 5, 6, 7 and 30) and the entire complex is slung from the radial masses at two points which lie mid-way between the two rings of muscles so that they can act in apposition (Text-figs. 5, 6 and 7). This can also be seen when the radial masses are studied from the outer surface of the head. Although the lips fuse externally relatively far anteriorly there is no fusion of the internal structures for some considerable distance posterior to this point. That is not until the level, roughly, of the radial processes. This arrangement is present in all the species studied and is also well shown in Ditlevsen's (1919) figure of *Enoplolaimus latignathus* (Ditlevsen's Plate XIII, Fig. 1). Thus the mandibular : onchial complex is slung from the radial masses so that the rotation line passes between the insertions of Muscles-1 and -2 and those of Muscles-3. The mandibles, therefore, are rotated under the action of muscles on the onchial plate and do not themselves have any muscle supply. The arrangement of the muscles of the anterior ring, Muscles-1 and Muscles-2, may indicate that they have arisen in response to the presence of three components in the mandibular complex but it is not possible to establish, or refute, this possibility until a more divided complex has been studied. I suspect, rather, that the arrangement of the muscles is determined first by the presence of the duct of the oesophageal gland which divides the oesophageal musculature into two blocks and more anteriorly the presence of the onchia causes a division into four—Muscles-3 (two) and Muscles-4 (two)—and finally

the most anterior muscles, Muscles-1 and Muscles-2, are arranged so as to fit into the more posterior muscles so that the available space is fully utilized.

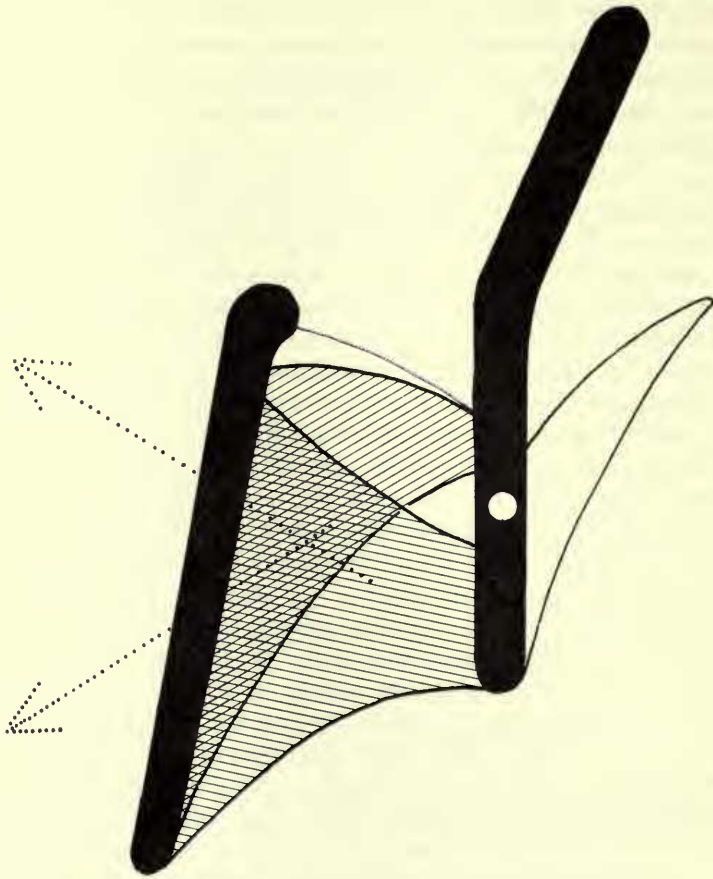


FIG. 8. Diagrammatic arrangement of the musculature of the mandibular : onchial-plate complex in the Enoplidae. The complex is to the right of the figure, the white dot represents the point of rotation of the complex and the arrows represent the approximate lines of action of the muscles.

THE STRUCTURE OF THE HEAD IN THE LEPTOSOMATIDAE

The structure of the head in this family has been considered by Wieser (1954) but, as pointed out above, he has over-looked some structural detail, particularly the presence of the cephalic ventricle, and I cannot accept his terminology and treatment of the so-called stomadaecal capsule. In general the head in this family is similar to those described in the other two families with a cephalic capsule and, in some cases, particularly *Thoracostoma*, there is a prominent cephalic ventricle.

The cephalic capsule in some genera is very strongly developed and a very distinct oesophageal capsule can also be present, for example in *Thoracostoma*, *Cylicolaimus*, *Macronchus*. In some cases a granular cervical capsule is also present. The elaborate arrangement of mandibles and onchia characteristic of the Enoplidae is never present. The most marked difference between this family and the others is in the way the musculature which supplies the various elaborations of the short buccal cavity extends anteriorly through the cephalic ventricle beyond the oesophageal capsule. To consider the structure of the head in the various species I have studied, in *Anticoma chitwoodi* there is a distinct cephalic capsule which, in one specimen, is pierced by several *lacunae* (Text-figs. 125-131). There is no cephalic ventricle and there is a single small onchium on each sector of the oesophagus (Text-figs. 122 and 125). There are no marked incisions in the cephalic capsule although in some cases the narrow fenestrae through which the nerves supplying the labial sense organs pass can be seen below the capsule. In *Parabarbonema* the cephalic capsule is well developed, without incisions. The amphidial openings lie on the posterior edge of the capsule, as in *Anticoma*, there is a slight cephalic ventricle, the mouth opening is tri-radiate and bounded by slight lip-lobes, the anterior end of each sector of the oesophagus is modified as a slight onchium which takes the form of a ridge of cuticle extending round most of each sector and the buccal cavity is very short (Text-figs. 132 and 133). The musculature which supplies the onchia can be seen arising within the anterior end of the oesophagus (Text-fig. 133) but due to the small size and poor condition of the specimens I have been unable to study its distribution in detail. It does, however, appear to represent a simple modification of the middle region of the musculature at the anterior end of each sector of the oesophagus. There are no incisions but six thin channels can be seen under the thickened cuticle of the cephalic capsule. There are six small lobes on the anterior edge of the cephalic capsule which lie in line with these fenestral channels (Text-figs. 132 and 133). The labial sense organs are papillate while the cephalic are setose (Text-fig. 137).

In *Macronchus* the cephalic capsule is very prominent but relatively narrow (Text-figs. 138, 139 and 141), there is a well developed oesophageal capsule and cephalic ventricle, the mouth opening is bounded by three lip-lobes (Text-fig. 143) and there is a large onchium developed from the middle of each oesophageal sector (Text-figs. 138 and 143). The muscles which supply the onchia form one mass, arising from the middle of each sector of the oesophagus at its anterior end, which passes anteriorly through the cephalic ventricle, as in *Parabarbonema*. The lining of the oesophageal lumen is strongly thickened at its anterior end (Text-fig. 141). The cephalic capsule has very slight incisions on its posterior edge and six fenestral channels can be seen beneath it. The onchia are flanked by a series of prominent wholly cuticular denticles which arise from a continuous basal sheet of cuticle which lines the shallow buccal cavity and is independent of the onchia and the oesophagus (Text-figs. 138, 139 and 141). In *en face* view, in deep focus, the distribution of the musculature which supplies the onchia can be seen rising as a mass from the middle of each sector of the oesophagus which is flanked by the spaces

of the cephalic ventricle (Text-fig. 140). In addition there is a narrow dense strip of cuticular material running from the outer end of each radius of the oesophagus to the periphery of the oesophagus. This structure is probably homologous with the radial mass in the Enoplidae. The result of the combination of these six structures, three muscle masses—which it should be noted are lying wholly within the head and do not project into the buccal cavity—and three radial strips, is that each nerve passing anteriorly comes to lie in a triangular space of the cephalic ventricle.

In *Thoracostoma* the cephalic capsule is very strongly developed with a prominent system of incisions, fenestrae and, in most cases, lacunae. The cephalic ventricle is very well developed and there appears to be a well developed oesophageal capsule in many cases. The oesophageal capsule and cephalic capsule are fused completely round their circumferences only at the anterior end and are attached to each other along three zones, which correspond to the three sectors of the oesophagus, posteriorly. Narrow strips of dense material run from the ends of the radii of the oesophageal lumen to the periphery of the oesophagus as in *Parabarbonema*. The anterior end of the oesophagus and the lining of the shallow buccal cavity are modified to form a variety of structures but when any of them is supplied with musculature this always arises from the anterior end of the oesophagus and passes forward as a narrow strip through the cephalic ventricle (Text-figs. 152 and 153). There are, therefore, two components in the anterior buccal armature, a true onchial one—such as the large bifurcate dorsal onchium in *T. jae* (Text-fig. 157)—and a buccal. In forms such as *T. zaeae* (Text-figs. 171 and 172) the large central structure on each ventro-lateral side of the buccal cavity is an onchium while the smaller flanking structures are derived from the cuticle lining the buccal cavity. Similarly the two ventro-lateral structures in the mouth of *T. jae* are onchia. The muscle supply to the similar large onchial structure developed on the dorsal side of the oesophagus is also shown by Wieser (1956, Fig. 1, c. page 245) in *T. bruuni* Wieser, 1956. In addition, in all three species there is a second, more posterior, wholly cuticular onchium developed from the covering of the dorsal sector of the oesophagus (Text-figs. 150, 154, 167 and 173). The anterior edge of the cephalic capsule is developed into six anteriorly directed lobes which correspond to the position of the nerves supplying the labial, papillate, sense organs. Wieser (1953 and 1956) refers to various lobes developed on the anterior edge of the cephalic capsule and six such structures are present on all three species I have seen. They are in all cases slightly serrate on their anterior edges the impression being that they are thinning and disappearing rather than that this reflects any specific character in their organization. The structure of these anterior lobes is difficult to establish with certainty since there appears to be an inner lobe from the oesophageal capsule accompanying them. I have shown such a structure in the figures (Text-figs. 152, 153, 167 and 168) but cannot be certain of its independent presence since it may simply represent the edge of the cephalic capsule lobe in optical section. The structure marked "stomadaecal ring" in Wieser's 1956 figures is the anterior part of the thickening of the oesophageal capsule seen in optical section and is not a distinct ring as in,

for example, *Enoplus*. The cephalic ring is, in all the specimens I have seen, a rather thin, lightly built structure (Text-figs. 150, 154, 168 and 169) which can only be seen with difficulty. The shape of the cephalic capsule and its associated incisions, fenestrae and lacunae has been used as major character in the delimitation of the various species of *Thoracostoma* but the extreme variation in some of the characters can be seen from Text-figs. 159-166 and 176-179. The systematic value and interpretation of these characters is considered fully later (page 330).

Two points remain to be considered. Schuurmans Stekhoven and Mawson (1955) and later Mawson (1958, 1958a) describe "three anterior processes from the helmet which come into relation with the stomatal lining at the angles of the buccal cavity" (Mawson, 1958a). I have not seen any such processes but they would appear to be represented by the cuticularization which stretches from the ends of the radii to the outer surface of the oesophagus. I would, therefore, interpret them as derivations from the oesophagus comparable to the radial masses of the Enoplidae. This is, however, by no means certain but it would appear to be most improbable that they are developments of the cephalic capsule itself. One result of this modification, however, is that anterior to the cephalic ring the vesicle is divided into six parts which are separated by the radii of the oesophagus and the structures connecting them to the outer surface and by the three anteriorly directed lobes of the oesophagus which supply the onchia (Text-figs. 156 and 173). It is this combination of characters which gives rise to the second point I wish to consider. Timm (1953) describes the presence of "six pairs of fine sclerotized pieces symmetrically arranged" round an anterior "cap" of oesophageal tissue in the female of *Leptosomatium acephalatum* Chitwood, 1936 and later describes similar structures from both sexes of *L. ranjhai* Timm, 1960. De Man (1893) describes similar structures from *L. elongatum* and Mawson (1958a) describes them from what she considers to be *L. arcticum* Filipjev, 1916. However, Timm (1953) points out that "The sclerotized pieces as figured appear broader than in totemount view due to their refractiveness when traced up and down.", this being in "The second cross section at 6 μ . . .". I am quite sure that what Timm is describing here is the same system as is shown in Text-figs. 156 and 173, that is, the lining of the cephalic ventricle, one component of each pair of sclerotized pieces corresponding to the musculature supplying the onchia and the other component corresponding to the radius of the oesophagus.

GENERAL DISCUSSION OF THE STRUCTURE OF THE HEAD

The structure of the head forms considered above may be treated as falling into two major groups which correspond to the two major forms of the oesophagus. The Enoplidae and Phanodermatidae in which the oesophagus is distinctly "cellular" or (another term) "Vesiculate" posteriorly and the Leptosomatidae in which it is wholly muscular posteriorly. The cellular appearance is easily recognized and is due to the musculature being concentrated into distinct bands. In the first two families the musculature of the oesophagus never extends anterior to the anterior limit of the cephalic capsule and the onchia, if present, always appear to project into the buccal or onchial cavities free from the surrounding structures. In the

Leptosomatidae the musculature of the oesophagus extends anterior to the cephalic ring, through the cephalic ventricle, the buccal cavity is relatively reduced and the musculature inserts inside the onchia and does not simply attach to the base as in the Enoplidae/Phanodermatidae—at least in the most highly specialized forms. The easiest way to see this difference is to compare the way in which the musculature is cut off sharply at the anterior end of the oesophagus in *Mesacanthion* (Text-figs. 16 and 17), for example, and how it extends anteriorly in, for example, *Thoracostoma jae* (Text-figs. 152 and 153). As a result the onchia in the Leptosomatidae tend to be carried much more anteriorly, relative to the mouth opening, than they are in the Enoplidae and Phanodermatidae so that the buccal cavity in the first family is shallow, but is deep in the other two families.

The primitive head form can be considered to be represented by the simple attachment of a form such as *Anticoma* with a cephalic capsule but no cephalic ventricle or any of the systems of rods or other elaborations. Such a head would probably have, or is best considered as having, a tri-radiate mouth opening without lips. Under such conditions the extent to which the mouth could open would depend on the opening of the lumen of the oesophagus, as is certainly true in, for example, some members of the Oxystomidae. As I have argued in considering the Subuluridae (Inglis, 1960), since the oesophagus acts as a pump and is a relatively dense organ, first the size of the particles which can pass down the lumen must be limited to the size of the open lumen and second the size of the mouth opening and the cross-sectional area of the buccal cavity must control the size of particle which can pass inwards to the oesophagus. Doncaster (1963) makes the same point about *Rhabditis oxycerca* and *Pelodera lambdiensis*, “The size of those (microbes) ingested is limited by the diameter of the stoma”. Now in the simple head of the *Anticoma* or *Crenopharynx*-type there is no such method of selection available and it appears certain that there is an evolutionary advantage in the appearance of such a preliminary sampling zone. In addition the simple mouth opening must have little flexibility. This would also be improved by separating the mouth opening and the oesophagus. The separation of the mouth opening from the oesophagus is very common throughout the Nematoda but only in the Enoplida has a large cephalic vesicle appeared (although a similar modification appears to be present in many Tylenchida) and its appearance is probably casually related to the fusion of the oesophagus to the body wall (a similar modification appears to be present in the Tylenchida also). If an evolutionary trend from forms without to forms with a buccal cavity be accepted, as appears to be incontrovertible, whether on the line of the Phanodermatidae/Enoplidae or the Leptosomatidae, I would argue that the buccal cavity appeared by a migration outwards of the tissue lining the inner surface of the buccal cavity. Because of the presence of the fusion of the oesophagus and body wall this tissue would have been unable to extend its movement beyond the line of attachment so that it built up at the anterior end of the body to form the cephalic ventricle. The development of such a vesicle necessitates the development of some kind of supporting structure, particularly for the inner circle of sense organs, and this is represented by the buccal rods of *Dayellus* and *Phanoderma*. The origin of such rods is probably indicated by

the conditions in the head of *Crenopharynx* in which precursors of rods appear to be represented by the cuticular V-shaped structures flanking the oesophageal radii at its anterior end. Further increase in the depth of the buccal cavity with an increase in the density of its lining would produce a mandibular plate, the independence of the buccal rods (mandibular rods) is reduced, the mandibular component becomes functionally the dominant part of the system, the onchia are reduced and finally disappear with a concomitant reduction in the depth of the buccal cavity and the size of the cephalic ventricle. An originally supporting system becomes the major triturating system to the exclusion of the original system which is now reduced to acting as the area of insertion for the muscles which operate the mandibles.

To elaborate, I interpret the six-lobed mouth opening of *Phanoderma* as derivable from a three lobed system similar to that of *Crenopharynx*. Thus the pre-cursors of the buccal rods would be localized by the coalition of the ends of the radii of the oesophagus and the associated part of the buccal cavity. In *Dayellus* the presence of prominent buccal rods in association with a large cephalic ventricle is clearly seen while in *Phanoderma* the rods are still present although the ventricle is somewhat reduced. It is clear that these three head forms cannot be considered to represent any kind of series since, although *Phanoderma* could be derived from *Crenopharynx* by an increased cuticularization of the anterior end of the oesophagus, *Dayellus* appears to represent a specialized form in which the onchial component of the oesophagus is greatly reduced. It is difficult to draw any general conclusions about this family in view of the very small number of forms referred to it and the insufficiency of most of the descriptions of the head. Some minor observations on the relationships within it will be found in the systematic section of this paper (page 305).

The structure of the Enoplidae head, although it forms a remarkably uniform group, can be considered as an elaboration of the type found in the Phanodermatidae. Thus, if the sheet of cuticle lying between the buccal rods of the Phanodermatidae should become thicker and denser an Enoplidae head would, in broad outline, result. This I think is what has happened. With an increase in the size of the head the mechanical requirements of supporting the cuticle surrounding the buccal cavity would necessitate the development of an increase in the skeletal component and this is what the mandibular complex clearly does. That it also acts, in most cases, as a system of gripping organs or jaws cannot be doubted but its arrangement within the lips and its fixed relationship to the nerves and labial sense organs can best be interpreted as those of a skeletal system. With the development of such a skeletal system the appearance of massive buccal and onchial cavities is rendered possible with the associated complex of onchial plates, radial processes, radial masses and specialized musculature. With an increase in the thickness of the specialization of the wall of the buccal cavity the importance of the buccal/mandibular rods must be reduced as their functions are progressively taken over by the mandibular plate until they become fused with it, as in *Enoplolaimus*, and finally absorbed into it, as in *Mesacanthion* and *Africanthion*.

With the development of the mandibular : onchial complex a new level of organiza-

tion has been reached which has enabled a massive radiation to occur resulting in heads without onchia or onchial cavities and reduced buccal cavities as in *Enoplus*, heads in which the onchial cavity has become dominant with a reduction of the onchia, mandibles and buccal cavity, as in some *Trileptium*, heads in which the mandibular cavity has become dominant with a reduction in the size of the onchial cavity and the onchia, as in *Rhabdodemanina*, heads in which the onchial component dominates with a great reduction or even complete loss of the mandibular component, as in *Oxyonchus* and heads in which the onchial component has dominated with reduction of the other components to minor supporting roles, as in *Thoracostomopsis*. It is clear from what I have just said that I am considering a head form such as that in *Enoplolaimus* as a morphotype or at least in some way median for the Enoplidae. This is simply for convenience since it supplies a good generalized head form which shows all the morphological features of the Enoplidae head in a reasonably well developed form. But to treat this as a primitive head type would be a mistake, it is only a generalized type. Wieser (1953) illustrates what he calls "... some interesting trends of progressive or regressive development with regard to the structure of the buccal cavity ..." and derives all the head forms from *Enoplolaimus*. This is not necessarily correct. It is noticeable that in the family the onchia can occur in two major ways, either they are all equal or the dorsal is smaller than the two, equal, ventro-lateral onchia. In the group with unequal onchia there are four obvious genera, *Savaljevia* Filipjev, 1927—with very poorly developed or no mandibular component and very long onchia; *Parasavaljevia* Wieser, 1953—with a well developed mandibular component with distinct mandibular rods and very long onchia; *Oxyonchus* Filipjev, 1927, with a well developed mandibular complex with distinct mandibular rods and shorter onchia which do not extend beyond the anterior end of the mandibular complex and *Enoplonema* Kreis, 1934, with mandibles which are well developed anteriorly and in which the onchia are short. Wieser (1953) treats this series as running *Oxyonchus* (with *Enoplonema* and *Paranoplus* as side branches)—*Parasavaljevia*—*Savaljevia* but there is more evidence to support the reverse interpretation, *Savaljevia*—*Parasavaljevia*—*Oxyonchus* since such a line could have originated with a Phanoderma-like form with unequal onchia and no mandibles and be thought of as a line along which the onchia have become reduced in size as the mandibular complex increased in importance. The relationship of *Paranoplus* Filipjev, 1927 to this group must, on the basis of what little evidence there is, be considered very doubtful while the status and relationships of *Enoplonema*, which is only known from Kreis's (1928) description of *Enoplonema* [= *Filipjevia*] *macrolabiatum*, must remain uncertain until a fuller and more detailed description is available. The other relationships Wieser suggests appear to be as well founded as is possible. That is, *Mesacanthoides*, Filipjev, 1927, *Enoploides* Savaljev, 1912, *Metenoploides* Wieser, 1953, and *Enoplus* Dujardin, 1845 represent a related group of genera. But I cannot understand the supposed differences between *Epacanthion* Wieser, 1953 and *Mesacanthion* Filipjev, 1927. Wieser says (on page 79) of *Epacanthion*, "The mandibles form an intermediate stage between *Enoploides* and *Mesacanthion*." but on page 58 he shows *Mesacanthion* linking *Enoplolaimus* and *Oxyonchus*. So

far as I can make out the mandibles in *Mesacanthion* sensu Wieser, 1953 are similar to those I have found in *Africanthion* while those of *Epacanthion* are similar to those I have found in the three species I refer to *Mesacanthion*, but see page 310. The apparently simple arrangement of genera set out by Wieser is further complicated by the occurrence of genera such as *Trileptium* Cobb, 1933, *Hyalacanthion* Wieser, 1959 in which the middle part of the mandibles is a thin sheet of cuticle, *Rhabdodemia* Baylis and Daubney, 1926, and *Trichenoplus* Mawson, 1956 (of which *Lyranema* Timm, 1961 is clearly a synonym).

Because of this elaboration and variation in the degree of development of the various components of the head it is not possible to arrange them in any significant sub-groups or even to suggest any lines of modification which have any objective significance. Every combination of characters appears to have been developed and much more information is required before anything approaching a reasonable grouping of the forms can be attempted. It does appear possible that the head structures have arisen from more than one source. That is, that the family Enoplidae as at present constituted is artificial and includes two, or even more, convergent groups. Nevertheless, it is clear that the genera *Enoplus* and *Enoploides* represent related groups which have been derived from groups with much more prominent onchia. We have here the derivation of a group with reduced buccal and onchial cavities from forms in which these cavities and their associated onchia were well developed so that *Enoplus*, for example, represents an extreme of modification and efficiency with a most economic use of the minimum amount of material. But, since I interpret the origins of such onchiate groups with large cavities to be from forms in which such elaborations were not present, along at least one line of evolution there has been first an elaboration of the buccal and onchial cavities and a later reduction. This regression of an earlier elaboration appears to have been the result of the reversal of the direction of tissue migration. This I have argued was probably from the interior of the buccal cavity outwards in the first stage of elaboration but has probably been by an inwards movement and condensation in the second stage, leading to the loss of the onchia and the condensation of the mandibles. This inward migration of tissue reduces the size of the buccal cavity and the cephalic vesicle and leads to an associated reduction and final suppression of the onchia. It also appears to have affected the distribution of the cephalic sense organs in that there is a definite tendency for a reduced onchial: mandibular complex to be associated with anteriorly situated cephalic setae, as in *Enoplus* and *Enoploides*.

If my interpretation of the origins of the head in the Enoplidae with its later condensation in at least one line be correct it shows an interesting parallel with the conditions occurring in some parasitic forms, *Porrocaecum ensicaudatum* (Zeder, 1800), for example, in which there is the appearance of an elaborate lip-pulp in the larvae and a subsequent simplification in the adult (Osche, 1958) while Chabaud (1959) argues a similar regression to explain the structure of the head in *Tetrameres americana* Cram, 1927, and in the genus *Cyrnea*. Chabaud has, however, extended the concept to cover in the first case the structure of the head in the larvae, the male and the female and in the second the argument is applied to a sequence of

species within a genus. I am extending the demonstration of this not unexpected phenomenon to apply to a series of genera.

In the Leptosomatidae the elaborate arrangement of mandibles and onchia characteristic of the previous family is never developed. This would appear to be associated with the way in which the onchia are developed from the oesophagus with musculature running anteriorly through the cephalic vesicle anterior to the cephalic ring. As a result no supporting structures have appeared in the buccal cavity, which is always small, in association with the nerves to the labial sense organs. Instead a comparable set of structures has been developed on the anterior edge of the cephalic capsule in, at least, *Thoracostoma* and *Parabarbonema*. Wieser (1954) employs the term "mandibles" in referring to the genera *Triodontolaimus*, and *Jagerskioldia* but the structures to which he refers are onchia. The further elaboration which flanks the onchia in genera such as these and *Thoracostoma* is always an elaboration of the wall of the buccal cavity and this cavity never attains the importance or size it reaches in the Enoplidae. Thus I interpret the Leptosomatidae as probably a group with little opportunity for further advance, other than minor specialization, because of the way in which the musculature of the onchia has developed. It is clear that the origins and importance of the Enoplidae, on the other hand, are dependent on the restriction of the musculature of the oesophagus to the posterior part of the head and it can—and will now—be argued that it is from this line that many of the other major groups of the Order have arisen.

Filipjev (1927) refers to the presence of pockets in the head of members of the Oncholaimidae but I have been unable to find any such structures in any of the genera of this family I have studied: *Oncholaimus*, *Prooncholaimus* (Inglis, 1962), and *Pontonema* (in this report). In all cases the musculature at the anterior end of the oesophagus is greatly reduced, in association with the development of a very large cavity, and is restricted to small strips running to the onchia (Text-figs. 184 and 185) and the inner layer of the cuticle at the anterior end of the body becomes markedly thicker from about the level of the amphidial opening anteriorly. This thickening is quite easily seen in uncleared specimens and frequently its posterior limit can be seen as a faint line running transversely round the body. Anteriorly, in *Pontonema*, the mouth capsule is fused to the outer cuticle of the body just anterior to the cephalic setae, once again showing as a faint line. This fusion does not originate along a simple transverse line but as six zones of fusion lying between the sense organs and the fusion is only complete round the head anterior to the labial sense organs. There are in effect six very wide foramina and when this region is studied the pocketed appearance described—and illustrated—by Filipjev results due to studying two zones of the head in optical section. The cephalic capsule is, therefore, still represented in this family by a thickening of the inner cuticle although the zone of attachment of the oesophagus and body wall has been reduced to a small anterior part and the cephalic vesicle has been completely reduced. Thus the large cavity at the anterior end of the Oncholaimidae is predominantly an onchial cavity and it must even be considered doubtful if any representative of the buccal cavity remains.

I interpret this type of head as a modification of the Enoplidae head in which the onchial cavity has come to dominate to the exclusion of all—or most—of the other components, as is argued by Filipjev (1934). Similarly the head in the Enchilidiidae can be interpreted as derived from the Enoplidae, although I am not sure about the relationships between the members of the Eurystominae and Enchilidiinae which look rather similar but are probably derived from very different sources.

The superfamily Tripyloidea of Chitwood (1950) and of Clark (1961) just cannot stand. The only character when Clark's classification is considered, which separates this group from the Enoploidea is "Cuticle of head not duplicate" particularly as his definition of the Enoploidea is "Cuticle of head duplicate: males with 0, 1 or 2 supplements". This superfamily appears to have been a dumping ground for many diverse difficult groups and since I have discovered the presence of a cephalic capsule and a cephalic slit in *Trissonchulus* (see Inglis, 1961) and in *Thalassironus* (present paper) the resemblances of the Ironidae to the Enoploidea become overwhelming. The form of the male tail and the structure of the head and anterior end of the oesophagus suggests affinities with some of the Leptosomatidae. The taxonomic treatment of these groups is considered below.

As a consequence of what I argue above there is a sequence in mouth form running: three-lobed—six-lobed—three large lips—six-lobed or no lobes (Enchilidiidae, ? *Rhabdodemanina*). Now Chitwood (1950) and de Coninck (1942) argue that the primitive mouth condition in the Nematoda is with six lips and they attempt to derive all other forms from this. I have already (Inglis, 1962) argued against this and shown that in the Subuluridae (Inglis, 1960) lip-lobes have appeared independently along at least three, and possibly four, evolutionary lines. Two principles were set out before, one—that as the mouth increases in size (that is, becomes more "open") there is an associated development of, or increase in the size and efficiency of, a triturating mechanism; and two—as the mouth opening increases in size the form taken by the bounding structures—lips—is determined by the mechanical requirements imposed by the cylindrical form of the body. This means that if the mouth opening is terminal—two dimensional (see above, page 274)—and the mouth is large it is most efficiently and strongly closed by a series of lip-lobes, usually six, while if it is closed by three they are most efficient when the mouth opening extends posteriorly to become three-dimensional so that bending of the lips takes place more posteriorly. The same functional requirements appear to have been met in the Enoplida. The primitive three-lobed mouth opening of forms such as *Anticoma* (even here there is an incipient division into six lobes) and *Crenopharynx* simply reflect the form of the oesophageal lumen posterior to them and their evolutionary modification with the appearance of a buccal cavity is discussed above (page 290) but when the mouth becomes large, as in the Enoplidae and Leptosomatidae it either extends posteriorly—as in the first family—or the lip structures are reduced to simple flaps of cuticle, as in the second family. The presence of six lip-lobes in the Oncholaimidae cannot on this basis be treated as a primitive condition but represents a modification to meet the functional demands imposed by the design of the body.

Thus the lip-lobes in forms such as *Pontonema* are not homologous with those of forms such as *Subulura ortleppi* Inglis, 1960 or *Allodapa baylisi* (López-Neyra, 1946) nor are three massive lips such as occur in the family Heterakidae (Inglis, 1957) and in the Ascaridoidea (Hartwich, 1952) homologous with the similar structures in the Enoplidae. I would argue that the so-called lips throughout the Nematoda are the expression of an evolutionarily plastic organ system reacting to similar functional demands in similar ways and that they have appeared and disappeared again and again along many different lines of evolutionary modification. This is most clearly established when the head is treated as a unit and Chitwood's (1950) errors in attempting to establish the homology of "lips" throughout the entire group have partly arisen from his methodology which is reflected by the separate treatment of "Cephalic Structures" and "Stoma". That the form of the mouth opening, its bounding structures and the type of oesophageal modification are linked as a functional unit is now absolutely clear and is most spectacularly demonstrated by the conditions in the Enoplidae in which the head, in spite of its morphological complexity, reduces to what is virtually one taxonomic character. This subject will be discussed more fully and generally elsewhere as it involves a consideration of the concepts of homology which I do not wish to go into here.

DEFINITIONS OF MORPHOLOGICAL TERMS

The following terms have all been employed above and are listed here, with their definitions, for convenience. The page on which they are first employed is given in parentheses together with the number of a figure in which the structure is illustrated.

Buccal cavity—that part of the lumen of the digestive tract, anterior to the end of the oesophagus, which leads to the mouth opening (page 271; Text-figs. 1 and 2)
Buccal rods—rods of dense material developed in the inner layers of the cuticle lining the buccal cavity which are associated with the nerves to the labial sense organs (page 271; Text-fig. 1).

Cephalic capsule—a zone at the anterior end of the body in which the inner layer of the cuticle is thick and dense (page 269; Text-figs. 1 and 2).

Cephalic ring—a transverse ring of dense cuticle at the anterior edge of the cephalic capsule (page 271; Text-figs. 1 and 2).

Cephalic slits—supplementary sense organs on the ventro-lateral aspect of the head in the families Enoplidae and Ironidae (page 273; Text-fig. 77).

Cephalic ventricle—the fluid filled space which occupies the body anterior to oesophagus (page 271; Text-fig. 1).

Cervical capsule—a zone of longitudinally striated or punctate cuticle lying posterior to the cephalic capsule in some species of Phanodermatidae and Enoplidae (page 272; Text-fig. 86).

Cirrus—a long club-shaped projecting modification of the cephalic slits (page 273; Text-fig. 59).

Fenestrae—large, generally circular, expansions of the incisions from which arise the cephalic sense organs (page 269; Text-fig. 1).

Incisions—strips of clear cuticle running anteriorly from the posterior edge of the cephalic capsule which correspond to the position of the nerves which supply the cephalic sense organs (page 269 ; Text-fig. 1).

Mandible—a supporting and/or gripping organ developed in the inner layers of the cuticle lining the median part of the buccal cavity in the Enoplidae (page 275 ; Text-fig. 3).

Mandibular plate—a zone of dense cuticle lying between the mandibular rods (page 278 ; Text-fig. 72).

Mandibular ring—the most posterior, radially extended thin ring of specialized cuticle associated with the mandibles (page 276 ; Text-fig. 30).

Mandibular rods—lateral components of the mandibles which are probably homologous with buccal rods (page 278 ; Text-fig. 72).

Odontium—a tooth-like structure developed from the lining of the buccal cavity (page 271 ; Text-fig. 171).

Oesophageal capsule—a zone of thickened cuticle capping the anterior end of the oesophagus (page 269 ; Text-fig. 1).

Onchium—a tooth-like structure developed from the anterior end of oesophagus (page 271 ; Text-fig. 2).

Onchial cavity—an expansion of the lumen of the anterior end of the oesophagus within which the onchia originate (plate 275 ; Text-fig. 2).

Onchial plate—the dense thickened cuticle lining the onchial cavity, in association with the origins of the onchi, on to which is inserted the specialized musculature at the anterior end of the oesophagus in the Enoplidae (page 276 ; Text-figs. 5-7).

Radial masses—dense blocks of material which develop within the oesophagus, at its anterior end, opposite the ends of the radii of the oesophageal lumen in the Enoplidae (page 277 ; Text-fig. 25).

Radial processes—narrow strips of dense cuticle running, in conjunction with the mandibular ring, from the onchial plate to the radial masses (page 277 ; Text-figs. 5-7).

Semi-lunar striations—striations on the lining of the buccal cavity covering a zone bounded posteriorly by the mandibular ring and anteriorly by a curved line running from the projecting tip of the mandible to the inter-labial space (page 275 ; Text-fig. 61).

SYSTEMATIC SECTION

RELATIONSHIPS WITHIN THE MARINE ENOPLIDA

The classification at present in use for the marine members of the Enoplida is still predominantly that of Filipjev (1927), a report which is still the best available on this group of nematodes. Wieser's (1953) publication is of the greatest value to anyone studying the group but his interests were different from those of Filipjev and few changes are made in the classification. Clark's (1961) classification is largely useful as a list of all the genera which are generally referred to the Order, although he has over-looked a few, for example in the Enoplidae (Enoplineae of Clark) : *Thoracostomopsis* Ditlevsen, 1919 and *Trileptium* Cobb, 1933, should be added ; in

the Leptosomatidae (-inae) : *Paraleptosomatides* Mawson, 1956 and three subgenera of *Thoracostoma*—*Pseudocella* Filipjev, 1927 ; *Corythostoma* and *Synonchoides* Wieser, 1956 should be added ; *Wieseria* Gerlach, 1956 should be added to the Oxystomidae (-inae), *Curvolaimus* Wieser, 1953 to the Oncholaimidae and *Gerlachystomina* Inglis, 1962 to the Eurystominae.

The Enoplida form a homogeneous group, which is also one of the most, if not the most, successful, of the Nematoda. The classification of at least the marine members is at present clearly unsatisfactory since it is artificial and does not reflect the phylogenetic interrelationships of the groups concerned. One major factor in the appearance of the group was the development of the attachment of the oesophagus to the outer wall of the body so that to use the presence or absence of a cephalic capsule or the presence or absence of the cephalic ventricle as a character is likely to lead to error since it could easily have, and almost certainly has, been lost along more than one evolutionary line. I am sure that originally such an attachment existed in all root stocks of the Enoplida and its absence in some forms is almost certainly due to its later loss not to it never having existed in an ancestral form. Within the marine members of the order, which are almost all referred to the Suborder Enoplina by Clark (1961), there appear to be at least two major evolutionary lines which do not correspond to the classification advanced by Filipjev, Chitwood or Clark. The division of the suborder into two Superfamilies Enoploidea and Tripyloidea cannot stand. The latter superfamily as constituted by Chitwood (1950) contains a heterogeneous group of genera from which Thorne (1939) removes the Alaimidae to the Dorylaimoidea. Clark (1961) removes the Mononchidae to the Dorylaimoidea and, creates a new Suborder Alaimina for the Alaimidae. As a result the superfamily Tripyloidea of Clark contains only two families, Trypylidae and Ironidae, of which the Ironidae form a remarkably uniform group characterized by a slight cephalic capsule and prominent solid onchia, the cephalic vesicle is lost, the buccal cavity is small, there is, in at least two genera—*Trissonchulus* and *Thalassironus*—a cephalic slit and the oesophageal glands empty near the anterior end of the oesophagus. All this demonstrates close relationship to the Enoploidea of Chitwood and Clark.

The Tripylidae which contains two genera, *Tripyla* Bastian, 1865 and *Tobrilus* Andrassy, 1959 is restricted to forms occurring in soil and freshwater and falls outside the limits of my discussion. It should, however, be pointed out that its relationships to other Enoplida are not clear and De Coninck (1935) includes *Tripyla* in the family Bastianidae of the Axonolaimida. Chitwood (1950) refers the Tripylidae to the Enoplida and the Bastianidae as an appendix to the Plectoidea. The relationships of this group are clearly uncertain. The same may be said of the Cryptonchinae Chitwood, 1937 which contains only one genus, *Cryptonchus* Cobb, 1913. This also is a freshwater group of uncertain relationships.

The Enoploidea, according to Clark, contains three families : Enoplidae, with four subfamilies, Enoplinae, Leptosomatinae, Phanodermatinae and Oxystominae ; Lauratonematidae, with no subfamilies and only one genus—*Lauratonema* Gerlach, 1953 and Oncholaimidae, with three subfamilies, Oncholaiminae, Eurystominae and

Enchilidiinae. This division appears to reflect convergent similarities rather than phylogenetic relationships. I would argue that a simple head form without a cephalic ventricle or any odontia or onchia is primitive to the Order. This is in agreement with the arguments of Filipjev (1934) who suggests "The Leptosomatidae are the simplest forms". As Filipjev also points out, the most primitive Oxystomatinae "are very similar to the Leptosomatidae" and the "Phanodermatinae in its simplest members,, closely resembles the Leptosomatinae as regards the structure of the head". Chitwood (1950) argues in the opposite way "In the Enoplidae stomata are definitely on the wane, being rudimentary in the Oxystomatinae and Phanodermatinae, represented chiefly by three mandibles in the Enoplineae and usually quite inconspicuous in the Leptosomatinae" and "Filipjev (1934) considered enoploids such as *Leptosomatum* which have no definite clear cut stoma as the more primitive while the writers regard forms such as *Rhabditis* and *Plectus* with distinct elongated stomata as primitive" and "Undoubtedly the Tripyloidea is the most primitive group of the order Enoplida, and hence most closely related to the Plectoidea. . . ." With all this I disagree strongly and am in complete agreement with Filipjev on the form of the most primitive heads.

The head in the Enoplidae is characterized by a complex of functionally interdependent characters which I have argued can be derived from the much simpler head forms found in the Phanodermatidae. In this I disagree with Filipjev (1934) who derives the Enoplineae from the Leptosomatinae by way of *Triodontolaimus*. The simplest forms in the Phanodermatidae approach the theoretical primitive head form and these two families appear to represent a natural group within which there are probably several evolutionary lines but the analysis of any such lines is not at present possible. There is a possibility that genera such as *Oxyonchus*, *Savaljevia* and *Parasavaljevia* represent an elaboration of the Phanoderma-type head which has developed independently of the other genera usually referred to the Enoplidae while *Enoplus* can be considered to represent the extreme in the development of the mandibular component of the head to the almost complete exclusion of the onchial along a (?) separate line including *Enoploides*, *Metenoploides* and, possibly, *Parenoplus*. The great difficulty in analysing this is the unsatisfactory grouping of species in the genera *Enoplolaimus*, *Mesacanthion*, *Enoploides* and *Paramesacanthion* (see page 310 for more detailed discussion) and until this can be unravelled the position must remain most unsatisfactory.

I consider the Oncholaimidae to be a group derived from the same broad Phanodermatidae: Enoplidae line which has radiated by the great expansion of the onchial component of the head with the almost complete suppression of the mandibular. Thus I interpret the large cavity of the Oncholaimidae as representing a great expansion of the onchial plate component of the Enoplidae. The Eurystomatinae and Enchilidiinae probably derived from the same line but they do not appear to be closely related to the Oncholaimidae. It is not clear how far they are themselves related since they probably represent the end results of massive convergence. The genus *Rhabdodemanina*, which is a rather peculiar group of species, is

probably nearer the Eursytominae: Enchilidiinae groups than it is to any other and could represent an ancestral type from which one of these subfamilies has been derived. It is, however, too specialised to give more than a hint in this direction and I shall continue to treat it here as a member of the Enoplidae.

The Leptosomatidae are clearly on a different evolutionary line from those discussed above. The form of the head is totally different with the oesophageal musculature passing far anteriorly and the buccal cavity developing, in the more advanced forms, a series of cuticular odontia. In this line also the simplest head forms are without buccal cavities or cephalic vesicles and the attachment of the oesophagus to the body wall is over a wide cap-like area at the anterior end. The specialization of the head appears to have prevented any massive change in the level of organization such as appears to characterize the derivation of the Oncholaimidae from the Enoplidae/Phanodermatidae line. Nevertheless it is possible that the Ironidae have been derived from this line in view of the similarities in the modification of the anterior end of the oesophagus, the form of the male tail and of the spicules. The position of this family must remain uncertain since the head could also—although I think less probably—have been derived from a form similar to that of the Enoplidae. I can make no observations on the Oxystomidae as I have not studied any members of this family but they appear to be somewhat similar to, and should later probably be classified with, the Leptosomatidae.

The general conclusions I draw are: 1—the Phanodermatidae/Enoplidae/Oncholaimidae form a related group, with the Eurystominae and Enchilidiinae probably derived from them. I would not, however, treat the latter subfamilies in the same family as the Oncholaimidae since I am sure their similarities are those of convergence. 2—the Oxystomidae : Leptosomatidae : Ironidae probably form a second related group. I am not prepared to advance any formal classification based on these ideas until I have had an opportunity to study more specimens, particularly of the Oxystomidae and Leptosomatidae. I shall therefore simply refer to the following families, Phanodermatidae, Enoplidae, Leptosomatidae, Enchilidiidae, Oncholaimidae and Ironidae.

LIST OF SPECIES DESCRIBED

The study reported above was based on specimens collected from South African waters among which are representatives of twenty four species, of which twenty two are described as new, belonging to eighteen genera, of which four are new, thus :

PHANODERMATIDAE

- Dayellus* gen. nov. (page 304).
- Dayellus dayi* sp. nov. (page 304).
- Crenopharynx* Filipjev, 1934 (page 306).
- Crenopharynx eina* sp. nov. (page 306).
- Crenopharynx afra* sp. nov. (page 308).
- Phanoderma* Bastian, 1865 (page 309).
- Phanoderma unica* sp. nov. (page 309).

ENOPLIDAE

- Oxyonchus* Filipjev, 1927 (page 311).
 Oxyonchus dittevseni sp. nov. (page 311).
Enoplolaimus de Man, 1893 (page 312).
 Enoplolaimus mus sp. nov. (page 312).
Mesacanthion Filipjev, 1927 (page 313).
 Mesacanthion cavei sp. nov. (page 313).
 Mesacanthion ceeus sp. nov. (page 314).
 Mesacanthion studiosa sp. nov. (page 315).
Africanthion gen. nov. (page 316).
 Africanthion nudus sp. nov. (page 316).
Trileptium Cobb, 1933 (page 317).
 Trileptium ayum sp. nov. (page 317).
Thoracostomopsis Ditlevsen, 1919 (page 318).
 Thoracostomopsis carolae sp. nov. (page 319).
Enoplus Dujardin, 1845 (page 320).
 Enoplus harlockae sp. nov. (page 320).
 Enoplus michaelsoni Linstow, 1896 (page 321).
Rhabdodemanina Baylis and Daubney, 1926 (page 322).
 Rhabdodemanina nancyae sp. nov. (page 322).

LEPTOSOMATIDAE

- Anticoma* Bastian, 1865 (page 324).
 Anticoma chitwoodi sp. nov. (page 324).
Parabarbonema gen. nov. (page 326).
 Parabarbonema barba sp. nov. (page 326).
Macronchus gen. nov. (page 328).
 Macronchus shealsi sp. nov. (page 328).
Thoracostoma Marion, 1870 (page 330).
 Thoracostoma angustifissulatum Mawson, 1956 (page 331).
 Thoracostoma jae sp. nov. (page 332).
 Thoracostoma zeae sp. nov. (page 334).

ENCHILIDIIDAE

- Eurystomina* Filipjev, 1918 (page 335).
 Eurystomina sudensis sp. nov. (page 335).

ONCHOLAIMIDAE

- Pontonema* Leidy, 1856 (page 336).
 Pontonema yaena sp. nov. (page 336).

IRONIDAE

- Thalassironus* de Man, 1889 (page 337).
 Thalassironus jungi sp. nov. (page 337).

SPECIES PRESENT IN EACH SAMPLE

The specimens studied were collected by hand from grab or trawl samples from a large number of localities. Unfortunately in many cases the material is so very badly preserved that it is impossible to study the specimens collected. Thus the numbers and distribution of the specimens and species can give little more than some vague indication of the populations sampled and the distribution and habitat preferences of the species present. The following list refers only to the samples studied during the taxonomic study and does not include any which were in poor condition. Details of the stations and of the Ecological Survey are given by Day (1961). The small number of species referable to orders other than Enoplida was described elsewhere (Inglis, 1963). The holotypes and some paratypes of all new species are deposited in the British Museum (Natural History) indicated by B.M. (N.H.) Reg. Nos. Representative specimens of each species, where possible, have been returned to the University of Cape Town.

False Bay Dredging (FAL)

FAL.392. 34° 12.6' S/18° 29.1' E. Khaki mud from 40 metres on 15.11.60.

Dayellus dayi (5♂♂, 3♀♀, 2 larvae).

FAL.408. 34° 08.8'S/18° 33.5' E. Khaki coloured sand from 32 metres on 16.5.61.

Dayellus dayi (1♂, 1♀).

South Coast Dredging (SCD)

SCD.212. 33° 58.8' S./25° 42.2' E. Coarse sand, broken shells from 26 metres on 24.11.60.

Crenopharynx eina (1♂, 3 larvae).

Mesacanthion cavei (1♂, 1 larva).

Mesacanthion ceus (1♂).

Trileptium ayum (1♂, 1♀, 1 larva).

Rhabdodemanian nancyae (10♂♂, 10♀♀).

SCD.220. 34° 02' S./23° 48.4' E. Sand, mud and rock from 50 metres on 29.11.60.

Dayellus dayi (2♂♂).

Anticoma chitwoodi (2♂♂, 1 larva).

SCD.233. 36° 28.5' S./21° 11.0' E. Khaki coloured sand from 182 metres on 4.12.60.

Crenopharynx afra (1♂, 1♀).

West Coast Dredging (WCD)

WCD.90. 32° 05' S./18° 17' E. Coarse white sand from 39 metres on 2.7.61.

Enoplolaimus mus (1♂, 1♀, 1 larva).

Africanthion nudus (6♀, 2 larvae).

Thoracostomopsis carolae (2♂♂, 1♀, 2 larvae).

Parabarbonema barba (12♂♂, 17♀♀, 29 larvae).

Macronchus shealsi (13♂♂, 11♀♀, 9 larvae).

- WCD.91. 32° 02' S./18° 17' E. Coarse white sand from 27 metres on 2.7.61.
Enoplolaimus mus (15♂♂, 19 larvae).
Mesacanthion cavei (1♂).
Mesacanthion studiosa (1♂).
Trileptium ayum (1♀).
Macronchus shealsi (1 larva).
Pontonema yaenae (10♂♂, 5♀♀, 3 larvae).
- WCD.93. 32° 05' S./18° 17' E. Coarse white sand from 39 metres on 2.7.61.
Phanoderma unica (1♂).
Africanthion nudus (2♂♂, 4♀♀, 1 larva).
Thoracostomopsis carolae (1♀).
Parabarbonema barba (6♂♂, 3♀♀, 3 larvae).
Rhabdodemia nancyae (3♂♂, 5♀♀, 4 larvae).
Macronchus shealsi (15♂♂, 18♀♀, 22 larvae).
Thalassironus jungi (2♂♂, 1♀).
- WCD.94. 32° 05' S./18° 16' E. Khaki coloured mud from 54 metres on 2.7.61.
Oxyonchus dittelevseni (1♂).
Enoplolaimus mus (1♂, 2♀♀).
Thoracostomopsis carolae (1♂, 2♀♀).
Parabarbonema barba (3♂♂).
Macronchus shealsi (11♂♂, 12♀♀, 8 larvae).
Eurystomina sudensis (2♂♂, 1♀).
Rhabdodemia nancyae (6♂♂, 8♀♀, 3 larvae).
Thalassironus jungi (3♂♂, 11♀♀, 5 larvae).
- WCD.99. 32° 16' S./18° 17' E. Coarse white sand from 27 metres on 2.7.61.
Enoplolaimus mus (1♀, 2 larvae).
Mesacanthion studiosa (2♂♂, 2♀♀, 2 larvae).
Enoplus harlockae (1♂).
Enoplus michaelsoni (1♂, 1 larva).
Thoracostoma angustifissulatum (1♂).
Thoracostoma jae (6♂♂, 5♀♀, 5 larvae).
Thoracostoma zae (1♂, 3 larvae).
Pontonema yaenae (4♂♂, 3♀♀, 2 larvae).
- WCD.102. 32° 05' S./18° 16' E. Khaki mud from 54 metres on 2.7.61.
Macronchus shealsi (5♂♂).

DESCRIPTIVE SECTION

Family PHANODERMATIDAE Filipjev, 1927

Currently eight genera, the limits of which are in many cases most uncertain, are referred to this family. I do not intend to discuss them here but I would point out that although the majority are considered to differ in the structure of the head most of the available descriptions are quite insufficient to allow its form to be established. This difficulty has become most pressing in relation to the new genus,

Dayellus, which I erect below. The presence of buccal rods or their pre-cursors has now been established in three genera, *Phanoderma*, *Crenopharynx* and *Dayellus*, and it appears probable that this is a common character throughout the family which may be diagnosed thus :

Enoplida : oesophagus "cellular"; mandibles never present ; cephalic capsule and cephalic vesicle not massive ; pre-cloacal supplement(s) usually tuboid. Type genus : *Phanoderma* Bastian, 1865.

Four species, belonging to three genera, referable to this family are present in the collections, thus :

DAYELLUS gen. nov.

Dayellus dayi gen. et sp. nov.

(Text-figs. 38-42)

MATERIAL STUDIED. 5 ♂♂ (1 selected as holotype), 3 ♀♀, 2 larvae (1 late 4th-stage). 34° 12.6' S./18° 29.1' E. on 15.11.60 from khaki mud at a depth of 40 metres (FAL 392). B.M. (N.H.), Reg. Nos. 1963. 184-193.

1 ♂, 1 ♀. 34° 08.8' S./18° 33.5' E. on 16.5.61 from fine khaki coloured sand at a depth of 32 metres (FAL 408). B.M. (N.H.), Reg. Nos. 1963. 194-195.

2 ♂♂. 34° 0.2' S./23° 48.4' E. on 29.11.60 from sand, mud and rock at a depth of 50 metres. SCD 220 (returned to Cape Town).

	Ratios			V	Body Length (mm.)
	a	b	c		
Males	63.6	5.8	19.4		6.8
	59.2	6.0	20.8		7.7
	65.0	6.2	23.6		7.8
	60.7	6.3	23.0		8.5
	74.6	6.6	24.8		9.7
Females	65.4	7.0	25.0	44.7	8.5
	62.1	6.7	24.7	45.6	8.7
	64.3	6.9	25.0	44.4	9.0
Larvae	69.0	6.8	21.6		6.9
	67.3	6.2	23.9	52.7	7.4 (4th-stage)

MEASUREMENTS (in mm. in order of body lengths). *Male*. Body breadth : 0.11 ; 0.13 ; 0.12 ; 0.14 ; 0.13. Oesophageal length : 1.18 ; 1.28 ; 1.25 ; 1.35 ; 1.46. Diameter of head : 0.010 ; 0.011 ; 0.009 ; 0.011 ; 0.012. Diameter of cephalic capsule at posterior edge : 0.016 ; 0.017 ; 0.013 ; 0.017 ; 0.018. Depth of cephalic capsule : 0.009 ; 0.009 ; 0.008 ; 0.009 ; 0.010. Length of cephalic setae : 0.022 and 0.019 ; 0.022 and 0.019 ; 0.022 and 0.020 ; 0.021 and 0.017 ; broken. Distance of nerve ring from anterior end : 0.327 ; 0.336 ; 0.331 ; 0.339 ; 0.366. Distance of excretory pore from anterior end : 0.069 ; 0.078 ; 0.074 ; 0.080 ; 0.081. Tail length : 0.35 ; 0.37 ; 0.33 ; 0.37 ; 0.39. Cloacal diameter : 0.064 ; 0.067 ; 0.075 ; 0.081 ; 0.084. Length of spicules : 0.126 ; 0.131 ; 0.135 ; 0.144 ; 0.135. Length of gubernaculum : 0.048 ; 0.050 ; 0.049 ; 0.051 ;

0.051. Length of pre-cloacal supplement : 0.027 ; 0.029 ; 0.026 ; 0.027 ; 0.028. Distance of pre-cloacal supplement anterior to cloacal opening : 0.042 ; 0.045 ; 0.045 ; 0.045 ; 0.048.

Female. Body breadth : 0.13 ; 0.14 ; 0.14. Oesophageal length : 1.28 ; 1.30 ; 1.30. Diameter of head : 0.011 ; 0.009 ; 0.010. Diameter of cephalic capsule at posterior edge : 0.017 ; 0.015 ; 0.016. Depth of cephalic capsule : 0.010 ; 0.010 ; 0.010. Length of cephalic setae : 0.025 and 0.022 ; 0.025 and 0.022 ; 0.026 and 0.023. Distance of nerve ring from anterior end : 0.387 ; 0.354 ; 0.356. Distance of excretory pore from anterior end : 0.074 ; 0.073 ; 0.071. Tail length : 0.34 ; 0.36 ; 0.36. Anal diameter : 0.081 ; 0.073 ; 0.075. Distance of vulva from anterior end : 3.8 ; 4.1 ; 4.0.

Larvae. Body breadth : 0.10 ; 0.11. Oesophageal length : 1.02 ; 1.25. Diameter of head : 0.099 ; 0.010. Diameter of cephalic capsule at posterior edge : 0.014 ; 0.015. Depth of cephalic capsule : 0.008 ; 0.008. Length of cephalic setae : 0.018 and 0.016 ; 0.018 and 0.017. Distance of nerve ring from anterior end : 0.324 ; 0.312. Distance of excretory pore from anterior end : 0.072 ; 0.063. Tail length : 0.32 ; 0.31. Anal diameter : 0.063 ; 0.075. Distance of vulva from anterior end in second larva : 3.9.

The head is similar to that of *Phanoderma* in possessing both a stomodaeal and a cephalic capsule, a mouth opening bounded by six indistinct lip-lobes, which are supported by the buccal rods, a triangular buccal cavity in cross section and an outer circle of ten long cephalic setae of which six are long and four are short. The anterior end of the body is, in many of the specimens, set-off by a constriction which appears to coincide with the posterior edge of the cephalic capsule. This constriction may be an artefact as it is not present in all the specimens. Due to the poorish condition of the specimens the exact outline of the capsules cannot be wholly established but the stomodaeal capsule definitely enfolds the lateral setae as shown in Text-fig. 38 while the cephalic capsule is straight posteriorly and terminates posterior to the cephalic setae (Text-figs. 38 and 41). The anterior end of the oesophagus is simple and has the typical cellular appearance posteriorly.

The tail terminates in a narrow flagellate portion in both sexes. In the male the spicules are equal in length and identical in structure. They are short with bluntly capitate posterior ends and are without alae. The gubernaculum is fairly massive with a pair of stout, bluntly rounded apophyses and a pair of thin, lightly built, lateral rods which project laterally and anteriorly (Text-figs. 40 and 42). There is a single, simple, rod-like pre-cloacal supplement which lies a relatively short distance anterior to the cloacal opening. Possibly because of the condition of the specimens no setae have been seen on the tail. The caudal glands lie posterior to the cloacal opening and there appear to be two opposed testes. The sperm are flagellate.

The female reproductive system is double with reflexed ovaries which lead into relatively large uteri which appear to be modified distally as spermathecae. The eggs are large and elongate, 0.20×0.099 mm. and 0.23×0.090 mm. being typical examples.

DISCUSSION

This species does not appear to be congeneric with any others referred to the family Phanodermatidae. It probably approaches the genus *Phanodermella* Kreis, 1928 most closely but differs from it in the form of the gubernaculum and (?) the structure of the head. The new genus, *Dayellus*, may be diagnosed thus :

Phanodermatidae : mouth opening surrounded by six-lobes supported by six buccal rods ; cephalic vesicle prominent ; no onchia are present ; cephalic capsule simple ; both cephalic and oesophageal capsules small ; cephalic setae relatively long.

Male. Spicules short ; pre-cloacal supplement present ; gubernaculum with a massive dorsal apophysis.

TYPE SPECIES : *Dayellus dayi* sp. nov.

Crenopharynx Filipjev, 1934

The systematic relationships of this genus are discussed by Schuurmans Stekhoven (1950) and Allgén (1932) who conclude that it shows similarities with the Leptosomatidae rather than the Phanodermatidae where it is placed by Filipjev (1934). With this suggestion Wieser (1953) disagrees, arguing with Filipjev that it should be included in the Phanodermatidae, an argument which I fully accept. Schuurmans Stekhoven compares it with *Anticoma* and argues that the two genera should be within the same family. However, I would interpret the points of similarity as relatively primitive characters and argue that the two genera have them in common because they are both somewhat primitive in structure. *Crenopharynx* clearly belongs with the Phanodermatidae because of the cellular form of the oesophagus and also the form of the head, while *Anticoma* (see page 324) for similar reasons should be referred to the Leptosomatidae.

The genus *Crenopharynx* may be diagnosed thus :

Phanodermatidae : mouth opening tri-radiate ; incipient buccal rods present ; prominent muscular onchia (?) present ; buccal cavity fits close to onchia ; cephalic vesicle small ; cephalic capsule lightly built ; oesophageal capsule not seen.

MALE : spicules long, narrowing rapidly towards the distal end ; barb usually developed at point where spicule narrows ; gubernaculum small and close lying.

TYPE SPECIES : *Anoplostoma gracile* Linstow, 1900.

Crenopharynx eina sp. nov.

(Text-figs. 43-44, 47-49)

MATERIAL STUDIED. 1 ♂ (holotype) ; 3 larvae. 33° 58·8' S./25° 42·2' E. on 24.II.60 from sand and broken shells from a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 272-275.

	Ratios			Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	
Male	29.1	4.3	18.9	6.4
Larvae	31.4	3.4	13.8	4.4
	26.8	3.9	16.2	5.1
	32.2	4.1	17.7	5.8

MEASUREMENTS (in mm. in order of body lengths). Body breadth : 0.22 ; 0.14 ; 0.19 ; 0.18. Oesophageal length : 1.49 ; 1.28 ; 1.31 ; 1.42. Diameter of head : 0.019 ; 0.016 ; 0.013 ; 0.017. Diameter of cephalic capsule at posterior edge : 0.026 ; 0.021 ; 0.022 ; 0.023. Depth of cephalic capsule : 0.012 ; 0.011 ; 0.011 ; 0.012. Length of cephalic setae : 0.013 and 0.018 ; 0.014 and 0.016 ; 0.010 and 0.014 ; 0.013 and 0.017. Distance of nerve ring from anterior end : 0.56 ; 0.54 ; 0.55 ; 0.58. Distance of excretory pore from anterior end : 0.18 ; 0.14 ; 0.16 ; 0.15. Tail length : 0.339 ; 0.318 ; 0.315 ; 0.328. Cloacal or anal diameter : 0.110 ; 0.084 ; 0.099 ; 0.099. Length of spicules : 0.463. Length of gubernaculum : 0.074.

The head is small and blunt (Text-fig. 49) and the oesophagus is typical, thin anteriorly and cellular posteriorly. The tail is relatively short and stoutish (Text-fig. 47) with the caudal glands lying posterior to the cloacal opening.

The spicules are equal in length and identical in structure. They are long and thin, expanding very slightly just anterior to the point at which they suddenly narrow very markedly to terminate in the long narrow tip which is apparently a diagnostic character of the genus (Text-fig. 47). Just at the point where they narrow is a small, but distinct, sharp pointed barb which is directed towards the distal end of the spicule. The gubernaculum is rather large with distinct lateral processes at the distal end (Text-fig. 48). There are two opposed testes.

DISCUSSION

The genus *Crenopharynx* currently contains six species, *C. gracilis* (Linstow, 1900) type species, *C. brevicaudatus* (Schuurmans Stekhoven, 1950), *C. crassus* (Ditlevsen, 1930), *C. marioni* (Southern, 1914), *C. metagracilis* (Schuurmans Stekhoven, 1950) and *C. paraleptus* (Schuurmans Stekhoven, 1950) of which *C. brevicaudatus* (not *C. brevicauda* as mis-spelt by Wieser, 1953) and *C. metagracilis* are insufficiently known for any comparison to be possible (they should probably be dismissed as *species dubia*). From the remaining species *C. eina* may be distinguished, apparently, by the presence of a distinct barb on the spicules although the description of *C. paraleptus* is insufficient to establish this. However, *C. eina* differs from that species, as well as all the others, in the shortness of the tail. It also differs from *C. marioni*, *C. crassus* and *C. gracilis* in the presence of lateral processes on the gubernaculum.

Crenopharynx eina is characterized by a relatively short tail, a barb on each spicule just anterior to the narrow terminal zone and the presence of lateral processes to the gubernaculum.

Crenopharynx afra sp. nov.

(Text-figs. 45-46)

MATERIAL STUDIED. 1 ♂ (holotype), 1 ♀. On 4.12.60 from khaki coloured sand from 182 metres at 36° 28.5' S./21° 11' E. (SCD 233). B.M. (N.H.), Reg. Nos. 1961. 276-277.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Male	53.1	3.3	14.7		6.9
Female	43.7	4.2	13.8	67.5	8.3

MEASUREMENTS (in mm., Male first, then Female). Body breadth : 0.13 ; 0.19. Oesophageal length : 2.10 ; 1.98. Diameter of head : 0.022 ; 0.023. Diameter of cephalic capsule at posterior edge : 0.030 ; 0.031. Depth of cephalic capsule : 0.017 ; 0.016. Length of cephalic setae : 0.010 and 0.011 ; 0.010 and 0.012. Distance of nerve ring from anterior end : 0.64 ; 0.68. Distance of excretory pore from anterior end : 0.18 ; 0.19. Tail length : 0.47 ; 0.60. Cloacal or anal diameter : 0.11 ; 0.14. Length of spicules : 0.447. Length of gubernaculum : 0.113. Distance of vulva from anterior end : 5.6.

This species is similar to the previous species in general structure. For example, the structure of the head and oesophagus, so far as can be determined, is exactly the same but it differs markedly in the shape of the tail which in this species terminates in a long flagellate portion (Text-fig. 45). The spicules, while having the same general shape, with a long narrow terminal portion, lack the distinct barb present in *C. eina*. This structure is here represented by a slight swelling of the spicules at approximately the same point along their lengths (Text-fig. 46). The form of the gubernaculum is also different. It is a rather slim structure which clings closely to the spicules, enclosing them along a good part of its length, and lacks the processes which are found in *C. eina* (Text-figs. 45 and 46). The eggs are 0.28 mm. × 0.19 mm.

DISCUSSION

This species is very similar to *C. crassus* (Ditlevsen, 1930) both in the shape of the tail and the shape of the gubernaculum. However, the form of the spicules cannot be established in Ditlevsen's species and I shall treat my specimens as, at least provisionally, distinct.

Crenopharynx afra is characterized by a long, flagellate tail, a lightly built gubernaculum with extensive lateral pieces and spicules without a definite barb near their posterior ends but having instead a slight swelling.

Phanoderma Bastian, 1865*Phanoderma unica* sp. nov.

(Text-figs. 50-54)

MATERIAL STUDIED. 1 ♂ 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres. (WCD.93). B.M. (N.H.), Reg. No. 1963. 58.

a	b	c	Ratios
			Body Length (mm.)
67.5	5.7	27.9	8.1

MEASUREMENTS (in mm.). Body breadth : 0.12. Oesophagus length : 1.43. Length of cephalic setae, long/short : 0.029/0.021. Cephalic capsule, length/diameter : 0.016/0.023. Distance of nerve ring from anterior end of body : 0.41. Distance of excretory pore from anterior end of body : 0.026. Distance of eye spots from anterior end of body : 0.054. Tail length : 0.29. Cloacal diameter : 0.093. Spicule length : 0.153. Gubernaculum length : 0.030. Distance of pre-cloacal supplement anterior to cloacal opening : 0.051.

No cervical capsule is present but eye spots are present. The structure of the head is typical (see above, page 271, and Inglis (1962)). The tail is fairly long, the spicules are short and stout without plates, the pre-cloacal supplement lies fairly close to the cloacal opening, the gubernaculum is complex with a massive double apophysis and the lateral pieces are developed as long embracing processes (Text-fig. 52). There is a median piece projecting between the spicules. Cephalic capsule very simple and straight posteriorly (Text-figs. 53 and 54).

DISCUSSION

This species appears to be distinct on the basis of the shape of the gubernaculum, the lack of a cervical capsule and the simplicity of the cephalic capsule but I am not happy about the present generic groupings within the Phanodermatidae. Many of the characters used appear to be those which could easily be over-looked or misinterpreted. Further, division of the genus *Phanoderma* on the basis of presence or absence of eye spots as is done by Wieser (1953) appears to be a division on a bibliographic rather than a biological character. The whole group is in drastic need of revision.

Family ENOPLIDAE Baird, 1853

This family represents a group of morphologically very similar genera and, probably because of their relatively great size, the structure of the various organ systems has been frequently studied. The major characters for the delimitation of genera have almost all come from the structure of the head. This, it has been shown above, forms a complex of interrelated and interdependent functional characters and it would, as a result, be liable to show considerable convergence in morphological structure. The major characters used in delimiting genera have been the form of the mandibles, the relative lengths of the onchia, the position of origin of the cephalic setae and, as a subsidiary character, the presence of striated

lips. For a discussion of the value of various other characters, for example the form of the spicules, the gubernaculum, and the pre-cloacal supplement, see Filipjev (1927) whose comments on their minor value appear to be well founded. The diagnosis of the family is fairly straight forward although there are some marginal groups to which some of the characters do not apply, but in general the following combination of characters occurs :

Enoplida : cephalic capsule and cephalic ring well developed ; cephalic ventricle prominent ; oesophageal musculature always stops posterior to cephalic and mandibular rings ; cephalic slit present ; three onchia usually present ; mandibular complex well developed ; buccal cavity usually well developed ; amphids not elongate ; oesophagus " cellular " due to restriction of musculature to distinct zones ; usually one tuboid pre-cloacal supplement.

TYPE GENUS : *Enoplus* Dujardin, 1845.

The delimitation of genera within the family is extremely complicated in view of the forms taken by the mandibles. In particular I suspect that the position of the cephalic setae relative to the cephalic ring is not a reliable character and that this varies along more than one line. Further, it is clear that at least three types of mandibular complex occur among the species currently referred to *Enoplolaimus*, *Mesacanthion*, *Enoploides* and *Paramesacanthion* and that species with the same type of mandible have been classified in different genera. This is not to suggest that the form of the mandible in itself is a rigid character for the allocation of species but it does appear to be a good indication of the degree of development of the other structures in the cephalic complex and may be taken as some indication of the other conditions in the head. Thus, the type of mandible in *Enoplolaimus mus* which I describe below, in which the mandibular rods are separate from the mandibular plate over a large part of their lengths, appears to be different from that found in the type species of *Enoplolaimus*, *E. vulgaris* de Man, 1893. In this latter species the mandibular rods appear to be wholly attached to the mandibular plate to produce a mandible of the type I describe for *Africanthion*. The *E. mus* type of mandible appears to be present in, for example, *E. lenunculus* Wieser, 1959, *E. paralitoralis* Wieser, 1959, *E. oxycephalus* Ditlevsen, 1926 (referred to *Mesacanthion* by Filipjev (1927) and then to *Paramesacanthion* by Wieser (1953)), *E. virilis* Ditlevsen, 1930 (referred to *Mesacanthion* by Wieser (1953)), and *Mesacanthion klugei* Filipjev, 1927. The more massive type of fused mandible, similar to that of *Africanthion*, appears to occur in, for example, *Enoplolaimus distortus* Gerlach, 1957, *E. connexus* Wieser, 1953, *Mesacanthion rigens* Gerlach, 1957, *M. infantilis* of Wieser, 1953 non *Enoplolaimus infantilis* Ditlevsen, 1930, *M. lucifer* Filipjev, 1927, and *M. africanum* Gerlach, 1957a. The most massive type of mandible, such as I describe here for three new species of *Mesacanthion*, appears to occur, for example, in *Mesacanthion breviseta* Filipjev, 1927, *M. major* Filipjev, 1927, *Enoploides amphioxi* Filipjev, 1918, *E. hirsutus* Filipjev, 1918, *E. brevis* Filipjev, 1918 and several other species which have been referred to *Enoploides* by various authors. This listing is not intended to be exhaustive but only indicative of the scale of the problem to be resolved. It appears almost certain that the family Enoplidae as at present con-

stituted contains several parallel lines of modification the members of which have been grouped on the basis of general morphological similarity rather than phylogenetically. A problem on this scale cannot be solved within the confines of a single report and I can only draw attention to it at this time. As a result the generic allocation of the species I describe below is based as far as possible on what appears to be the usual practice and largely on the generic groupings of Wieser (1953) which must for some time to come continue to supply the best practical basis for classification.

Oxyonchus Filipjev, 1927

This genus is characterized, particularly, by the presence of unequal onchia of which the longer ventro-lateral do not extend anterior to the anterior edge of the mandibular plate. It is morphologically very similar to *Savaljevia* Filipjev, 1927 and *Parasavaljevia* Wieser, 1953 but differs in the form of the mandibular complex and the length of the ventral onchia (see Wieser, (1953) for discussion). The genus may be diagnosed thus :

Enoplidae : mandibular rods separate from mandibular plate ; dorsal onchium small ; ventro-lateral onchia equal and large but not extending beyond anterior edge of mandibular plate ; series of small denticles developed from inner surface of mandibular plate ; cephalic setae arising from near cephalic ring ; spicules short and stout ; gubernaculum with apophysis ; pre-cloacal supplement small.

TYPE SPECIES : *Enoplolaimus hamatus* Steiner, 1916.

*Oxyonchus pachylabiatu*s Schuurmans Stekhoven, 1946 does not agree with this diagnosis since, according to Schuurmans Stekhoven, it lacks a supplement and an apophysis to the gubernaculum but his male specimen looks suspiciously like a 4th-stage larva.

Oxyonchus ditlevseni sp. nov.

(Text-figs. 55-59)

MATERIAL STUDIED. 1 ♂. 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. No. 1963. 129.

a	b	c	Ratios
			Body Length (mm.)
37.6	4.8	11.7	3.5

MEASUREMENTS (in mm.). Body breadth : 0.093. Oesophagus length : 0.73. Diameter of head : 0.033. Length of cephalic setae, long/short : 0.036/0.012. Tail length : 0.30. Cloacal diameter : 0.056. Spicule length : 0.060. Gubernaculum length : 0.033. Distance of pre-cloacal supplement anterior to cloacal opening : 0.127.

The head bears a well developed " cirrus " and the mandibles bear about sixteen small denticles arranged roughly in two rows. The cephalic setae are long and thin

with six longer than the remaining four. There are some thin, rather long setae arising from the body immediately posterior to the cephalic capsule (Text-fig. 55) the distribution of which is not clear since they are either very asymmetrical in their distribution or some have been lost.

The tail is long and narrow (Text-fig. 56) with a small pre-cloacal supplement lying relatively far anterior to the cloacal opening. The spicules are stout with narrow alae and blunt, square cut distal ends (Text-fig. 58). The gubernaculum is irregular in outline with distinctly square cut lateral pieces and a fairly prominent central piece which projects between the spicules (Text-fig. 58).

DISCUSSION

This species, on the basis of the length of the cephalic setae and the number of denticles in the mandibular fields, appears to be most similar to *Oxyonchus dentatus* (Ditlevsen, 1919) but differs from it in the blunt posterior tips to the spicules, the relatively longer tail and the form of the gubernaculum—so far as it is possible to establish this latter character on the basis of the available descriptions of *O. dentatus*.

Enoplolaimus de Man, 1893

The delimitation of this genus is most uncertain and a discussion of the difficulties is given above (page 310). The following species is referred to it because several similar species have been referred to it before.

Enoplolaimus mus sp. nov.

(Text-figs. 60–73)

MATERIAL STUDIED. 4 ♂♂ (1 selected as holotype), 2 larvae (+ 11 ♂♂, 17 larvae in very poor condition). 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.), Reg. Nos. 1961. 281–295.

1 ♂, 1 ♀, 1 larva (all in very poor condition). 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 90 (returned to South Africa).

1 ♀, 2 larvae (all in very poor condition). 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 296–298.

1 ♂, 2 ♀♀ (very poor condition). 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94).

a	Ratios		Body Length (mm.)
	b	c	
31.3	4.5	16.2	4.7
35.4	4.4	15.3	4.6
33.3	4.6	15.2	5.0
34.3	4.5	15.5	4.8

MEASUREMENTS (in mm. in order of body length above). Body breadth : 0.13 ; 0.15 ; 0.14 ; 0.15. Oesophagus length : 1.05 ; 1.04 ; 1.07 ; 1.09. Length of

cephalic setae, anterior/long posterior/short posterior : 0.017/0.105/0.055 ; 0.018/0.103/0.058 ; 0.018/0.105/0.057 ; 0.018/0.106/0.058 ; Cephalic capsule, depth/breadth : 0.045/0.060 ; 0.048/0.062 ; 0.047/0.064 ; 0.050/0.066. Length of onchia : 0.019 ; 0.018 ; 0.019 ; 0.021. Distance of nerve ring from anterior end of body : 0.29 ; 0.30 ; 0.32 ; 0.34. Tail length : 0.30 ; 0.29 ; 0.31 ; 0.33. Cloacal diameter : 0.084 ; 0.087 ; 0.088 ; 0.091. Spicule length : 0.083 ; 0.090 ; 0.091 ; 0.094. Distance of pre-cloacal supplement anterior to cloacal opening : 0.19 ; 0.23 ; 0.25 ; 0.26.

The specimens of this species are in most cases poorly preserved which is why measurements are given for males only.

The tail in the male is long and narrow and the small pre-cloacal supplement lies relatively far anterior to the cloacal opening (Text-fig. 71). The spicules are fairly massive and squarish in outline. They expand slightly towards their posterior ends where there is a small barb-like process just proximal of the blunt ends. The blunt distal ends are split into two plate-like processes of which the more lateral is folded proximally along the length of the spicule (Text-fig. 73). The gubernaculum is slim and simple and lie close to the spicules.

DISCUSSION

Enoplolaimus mus is characterized by the short, blunt spicules with their divided distal ends, the small pre-cloacal supplement lying a relatively long way anterior to the cloacal opening, the form of the tail and the lengths of the cephalic setae.

Mesacanthion Filipjev, 1927

It should be noted that in two of the species I refer to this genus a number of cervical setae occur on the males but none are found on females or larvae.

Mesacanthion cavei sp. nov.

(Text-figs. 76-78)

MATERIAL STUDIED. 1 ♂ (holotype), 1 damaged larva (from this specimen *en face* preparation was made). 33° 58.8' S./25° 42.2' E. on 24.II.60 from coarse sand and broken shells at a depth of 26 metres. (SCD 212) B.M. (N.H.), Reg. No. 1963. 278.

1 ♂ (very poor condition). 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres. WCD 91 (returned to South Africa).

a	Ratios		Body Length (mm.)
	b	c	
38.2	4.2	17.5	4.2

MEASUREMENTS (in mm.). Body breadth : 0.110. Oesophageal length : 1.00. Diameter of head : 0.060. Diameter of cephalic capsule at posterior end : 0.068. Depth of cephalic capsule : 0.052. Length of cephalic setae : 0.035 and 0.059. Length of anterior cephalic setae : 0.013. Distance of nerve ring from anterior

end : 0.23. Excretory pore not seen. Tail length : 0.24. Cloacal diameter : 0.064. Length of spicules : 0.51. Length of gubernaculum : 0.038. Length of pre-cloacal supplement : 0.019. Distance of pre-cloacal supplement anterior to cloacal opening : 0.161.

The spicules are equal in length and identical in structure with simple pointed posterior ends, without alae. The gubernaculum is fairly lightly built but is slightly more complex at the proximal end than in *M. ceus* although it clings close to the spicules along its whole length. The tail is relatively stout with, compared to *M. ceus*, a short terminal portion (Text-fig. 78).

DISCUSSION

M. cavei is characterized by long, simple spicules and a relatively short, stout tail.

Mesacanthion ceus sp. nov.

(Text-figs. 74-75)

MATERIAL STUDIED. 1 ♂ (Holotype), 1 larva. 33° 58' S./25° 42.4' E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 1961. 279-280.

	<i>a</i>	Ratios <i>b</i>	<i>c</i>	Body Length (mm.)
Male	41.7	4.9	13.5	3.5
Larva	41.4	5.0	14.2	3.7

MEASUREMENTS (in mm. in order of body lengths). Body breadth : 0.084 ; 0.087. Oesophageal length : 0.71 ; 0.74. Diameter of head : 0.063 ; 0.058. Diameter of cephalic capsule at posterior end : 0.056 ; 0.051. Depth of cephalic capsule : 0.059 ; 0.059. Length of cephalic setae : . . . ; 0.021 and 0.034. Distance of nerve ring from anterior end : 0.18 ; 0.19. Excretory pore not seen. Tail length : 0.28 ; 0.26. Cloacal or anal diameter : 0.048 ; 0.051. Length of spicules : 0.43. Length of gubernaculum : 0.031. Length of pre-cloacal supplement : 0.018. Distance of pre-cloacal supplement anterior to cloacal opening : 0.121.

The spicules are equal in length and identical in structure with distinct alae on their posterior ends which stop slightly anterior to the extreme posterior tips. The gubernaculum is very lightly built and clings very close to the spicules. The tail is relatively long and narrow, relative to *M. cavei*, and the caudal glands lie posterior to the cloacal opening (Text-fig. 75).

DISCUSSION

M. ceus is characterized by the alate form of the spicules and the relatively long narrow tail. No cervical setae are present on the male specimen but this may not be a character of any significance since there are no cephalic setae present either which suggests that all the long setae have been lost.

Mesacanthion studiosa sp. nov.

(Text-figs. 79-90)

MATERIAL STUDIED. 2 ♂♂ (1 selected as holotype), 2 ♀♀, 2 larvae. 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 196-201.

1 ♂. 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand from a depth of 27 metres. WCD 91 (returned to South Africa).

	Ratios				Body Length
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	(mm.)
Males	48.4	4.3	18.7		5.5
	48.3	4.1	16.0		5.8
	53.7	4.3	16.4		5.9
Females	51.7	4.5	18.8	53.2	6.2
	52.3	4.7	20.6	55.9	6.8
Larvae	48.5	3.9	16.2		4.5
	50.0	4.1	16.0		4.8

MEASUREMENTS (in mm. in order of body lengths above). *Males*. Body breadth: 0.11; 0.12; 0.11. Oesophagus length: 1.36; 1.40; 1.38. Lengths of cephalic setae, anterior/shorter posterior/longer posterior: 0.020/0.020/0.050; 0.019/0.019/not present; 0.019/0.018/0.048. Length of cervical setae: 0.030; 0.031; 0.031. Cephalic capsule, depth/diameter: 0.064/0.089; 0.070/0.087; 0.062/0.091. Tail length: 0.31; 0.30; 0.36. Cloacal diameter: 0.076; 0.081; 0.075. Spicule length: 0.068; 0.081; 0.075. Distance of pre-cloacal supplement anterior to cloacal opening: 0.132; 0.159; 0.129.

Females. Body breadth: 0.12; 0.13. Oesophagus length: 1.37; 1.46. Lengths of cephalic setae, anterior/shorter posterior/longer posterior: 0.022/0.018/0.043; 0.020/0.018/0.048. No cervical setae. Cephalic capsule, depth/diameter: 0.075/0.107; 0.070/0.096. Distance of nerve ring from anterior end of body: 0.33; 0.31. Tail length: 0.33; 0.33. Anal diameter: 0.075; 0.075. Distance of vulva from anterior end of body: 3.3; 3.8.

Larvae. Body breadth: 0.093; 0.096. Oesophagus length: 1.16; 1.17. Lengths of cephalic setae, anterior/shorter posterior/longer posterior: 0.014/0.014/0.042; 0.014/0.014/0.046. No cervical setae. Cephalic capsule, depth/diameter: 0.054/0.076; 0.058/0.080. Distance of nerve ring from anterior end of body: 0.27; 0.28. Tail length: 0.28; 0.30. Anal diameter: 0.069; 0.074.

The tail is of about an even breadth along most of its length in both sexes (Text-fig. 88). The spicules are short with bluntly rounded distal ends, are arcuate and about the same width all along their length. There is some slight variation in outline (see Text-figs. 81 and 82). There is no gubernaculum and the pre-cloacal supplement is small and simple lying about two spicule lengths anterior to the cloacal opening.

DISCUSSION

M. studiosa is characterized by the form of the spicules, the blunt tail and the small pre-cloacal supplement.

AFRICANTHION Gen. nov.

Diagnosis on page 317

Africanthion nudus sp. nov.

(Text-figs. 91-98)

MATERIAL STUDIED. 2 ♂♂, 4 ♀♀ (+ 1 larva in poor condition). 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 46-49 (1 ♂ returned to South Africa).

6 ♀♀, 2 larvae. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 50-57.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	41.8	3.9	50.6		7.1
	46.5	3.9	43.5		7.4
Females	37.8	3.2	40.0	66.1	6.8
	42.8	3.6	42.0	65.0	8.0
	42.0	4.4	46.3	64.8	8.8
	43.6	4.2	46.0	63.0	9.2

MEASUREMENTS (in mm., in order of body lengths above). *Males*. Body breadth: 0.17; 0.16. Oesophagus length: 1.81; 1.90. Cephalic capsule, length/breadth: 0.086/0.120; 0.070/0.107. Lengths of cephalic setae, anterior/longer posterior/shorter posterior: 0.028/0.090/0.048; 0.031/0.092/0.053. Length of mandibles: 0.027; 0.024. Distance of nerve ring from anterior end of body: 0.31; 0.29. Tail length: 0.14; 0.17. Cloacal diameter: 0.076; 0.072. Spicule length: 0.089; 0.080. Gubernaculum length: 0.032; 0.028.

Females. Body breadth: 0.18; 0.19; 0.21; 0.21. Oesophagus length: 2.16; 2.21; 2.00; 2.21. Cephalic capsule, length/breadth: 0.073/0.117; 0.087/0.126; 0.086/0.121; 0.082/0.123. Lengths of cephalic setae, anterior/longer posterior/shorter posterior: 0.027/0.087/0.042; 0.031/0.099/0.054; 0.031/0.096/0.051; 0.034/0.086/0.051. Length of mandibles: 0.027; 0.032; 0.033. Distance of nerve ring from anterior end of body: 0.28; 0.35; 0.30; 0.31. Tail length: 0.17; 0.19; 0.19; 0.20. Anal diameter: 0.096; 0.135; 0.108; 0.111. Distance of vulva from anterior end of body: 4.5; 5.2; 5.7; 5.8.

The structure of the head of this species is described in detail above (page 280) and is illustrated in Text-figs. 91, 92, 93, 95 and 98. It may be noted here, however, that as a diagnostic character the posterior position of the onchia relative to the mandibular arches is highly characteristic. There are many short setae on the anterior end of the body which become progressively less common posteriorly until about the level of and posterior to the nerve ring they are very rare.

The male tail is very characteristic. It is short and stout (Text-fig. 94) without a pre-cloacal supplementary organ of any kind. There is, however, a series of six stout short setae on the mid-ventral line of the body, about two spicule lengths anterior to the cloacal opening, which appear to replace the supplement found in this region in all other Enoplidae. There are, in addition, two files of more normal thin setae, ventro-lateral in position, running between the cloacal opening and the stout ventral setae (Text-figs. 94 and 96). The spicules are short, massive and curved at the distal ends where they finish in a sharp hook-like point (Text-fig. 97). The gubernaculum is small with a complex distal end and lies close to the spicules.

DISCUSSION

This species is apparently similar to those generally referred to the genus *Mesacanthion* but differs in the structure of the mandibles, the form of the male reproductive apparatus with the blunt spicules and elaborate, small gubernaculum and differs from all other Enoplidae in the presence of stout setae on the ventral surface of the male anterior to the cloacal opening in the area in which the pre-cloacal supplement is usually found. I, therefore, refer it to a new genus, *Africanthion*, which may be diagnosed thus :

Enoplidae : mandibles with lateral processes very well developed and mandibular walls fairly narrow in optical section ; mandibular plate thin ; onchia slightly unequal, dorsal smaller than ventro-lateral ; onchia lying far posterior to mandibles ; cephalic setae arising from middle of cephalic capsule.

MALES : spicules short and stout ; gubernaculum small and complex ; pre-cloacal supplement replaced by a file of stout, short setae.

TYPE SPECIES : *Africanthion nudus* sp. nov.

Trileptium Cobb, 1933

It is with some reservations that I refer the species described below to this genus but it appears to correspond to the descriptions which have been given by other authors sufficiently closely to warrant this allocation.

Trileptium ayum sp. nov.

(Text-figs. 99-102)

MATERIAL STUDIED. 1 ♂ (Holotype), 1 ♀, 1 ♀ 4th-stage larva, 1 larva. 33° 58.8' S./25° 42.2' E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos. 1963. 139-141.

1 ♀. 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91) (Very poor condition).

	Ratios				Body Length
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	(mm.)
Male	50.8	4.9	31.0		6.6
Female	48.8	4.6	28.2	63.9	8.3
Larva (♀)	47.5	4.6	32.8	49.1	5.7
Larva	41.7	3.4	24.0		3.5

MEASUREMENTS (in mm.). *Male* ; *female*. Body breadth : 0.13 ; 0.17. Oesophageal length : 1.34 ; 1.79. Diameter of head : 0.034 ; 0.045. Diameter of cephalic capsule at posterior edge : 0.042 ; 0.062. Depth of cephalic capsule : 0.036 ; 0.047. Length of cephalic setae : 0.024 and 0.081 ; 0.028 and 0.099. Distance of nerve ring from anterior end : 0.25 ; 0.20. Excretory pore not seen. Tail length : 0.213 ; 0.294. Cloacal or anal diameter : 0.075 ; 0.120. Length of spicules : 0.65. Length of gubernaculum : 0.058. Length of pre-cloacal supplement : 0.013. Distance of pre-cloacal supplement anterior to cloacal opening : 0.046. Distance of vulva from anterior end : 5.3. Cervical setae and long body setae were seen only in the male where they were 0.027 to 0.060 mm. and 0.049–0.054 mm. in length respectively.

Larvae (4th-stage ♀ first). Body breadth : 0.12 ; 0.084. Oesophageal length : 1.24 ; 1.03. Diameter of head : 0.039 ; 0.030. Diameter of cephalic capsule at posterior edge : 0.047 ; 0.025. Depth of cephalic capsule : 0.039 ; 0.029. Length of cephalic setae : 0.030 and 0.081 ; . . . and 0.037. Distance of nerve ring from anterior end : 0.024 ; 0.020. Excretory pore not seen. Tail length : 0.174 ; 0.146. Anal diameter : 0.072 ; 0.057. Distance of vulva from anterior end : 2.8.

The inner pouch of the cephalic slit is very prominent (Text-figs. 99 and 100) and the cephalic setae are very long. The amphids are small, lying just posterior to the posterior edge of the cephalic capsule, and slightly ventral in position. The mouth is closed by three small lip-flaps, the three onchia are small and lie far forward between the mandibles (Text-fig. 101), the cephalic capsule is poorly developed and there are several long cervical setae present on the male only. The tail is short and stout in both sexes (Text-fig. 102).

The spicules are long and thin, equal in length and without alae. The gubernaculum is small and clings close to the spicules while the simple pre-cloacal supplement lies relatively close to the cloacal opening (Text-fig. 102). There are two opposed testes.

The female reproductive system is double with reflexed, opposed ovaries. The eggs are large, 0.40 × 0.11 mm. in size.

DISCUSSION

The genus *Trileptium* currently contains four species, *T. subterraneum* (Gerlach, 1952), *T. salvadoriense* Gerlach, 1955, *T. gullata* (Cobb, 1920), *T. iacobinum* Wieser, 1959, from which the present species can be distinguished by the following combination of characters : pre-cloacal supplement present, gubernaculum without an apophysis, all three onchia present although rather small.

Thoracostomopsis Ditlevsen, 1919

Filipjev (1927) proposes a new subfamily for this genus because both he and Ditlevsen (1919) misunderstood the structure of the head and thought it contained a spear. Four species have been previously referred to the genus, *T. barbata* Ditlevsen, 1919 (type species) ; *T. ditlevseni*, *T. galeata* and *T. longissima* all three described and named by Filipjev (1927). Two of these species, *T. barbata* and

T. galeata, are only known on the basis of females. In view of the great similarities between the species I describe below and *T. barbata*, in the structure of the head, and the markedly different type of head described by Filipjev for his species it is possible that more than one genus should be recognized. The genus, although well founded and very distinct from any other, can only be treated as one of the several types of modification of the Enoplidae and certainly does not, at present, warrant separation in a distinct subfamily.

***Thoracostomopsis carolae* sp. nov.**

(Text-figs. 103–109)

MATERIAL STUDIED. 1 ♂ (Holotype), 2 ♀♀. 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 180–182.

1 ♀. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. No. 1963. 183.

1 ♂ (+ 1 ♂, 1 ♀ in poor condition). 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 90 (returned to South Africa).

	Ratios				
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	Body Length (mm.)
Males (holotype)	75.5	10.0	39.4		8.3
	67.4	9.3	31.2		8.1
Females	60.0	9.7	35.5	55.1	7.8
	63.1	10.0	39.4	54.7	9.5
	68.5	10.3	41.6	55.2	9.6

MEASUREMENTS (in mm. in order of body lengths above). *Males*. Body breadth: 0.11; 0.12. Oesophagus length: 0.83; 0.87. Mandible length: 0.012; 0.013. Cephalic capsule, length/diameter: 0.029/0.031; 0.031/0.033. Length setae, anterior/longer posterior/shorter posterior: 0.014/0.068/0.030; 0.013/0.065/0.032. Length of cervical setae on holotype: 0.032; 0.046. Tail length: 0.21; 0.26. Cloacal diameter: 0.071; 0.083. Spicule length: 0.165; 0.176. Gubernaculum length: 0.045; 0.067. Distance of pre-cloacal supplement anterior to cloacal opening: 0.141; 0.154.

Females. Body breadth: 0.13; 0.15; 0.14. Oesophagus length: 0.80; 0.85; 0.95. Mandible length: 0.014; 0.011; 0.012. Cephalic capsule, length/breadth: 0.028/0.033; 0.030/0.034; 0.032/0.035. Length of setae, anterior/longer/longer posterior/shorter posterior: 0.012/0.058/0.031; 0.014/0.063/0.029; 0.014/0.066/0.028. Tail length: 0.22; 0.22; 0.23. Anal diameter: 0.069; 0.067; 0.066. Distance of vulva from anterior end: 4.3; 5.2; 5.3.

The most spectacular morphological feature of this animal is the highly modified head and oesophagus which are described above in detail (page 281) and illustrated in Text-figs. 103–107. The anterior end of the body shows a slight sexual dimorphism in that there are several long setae just posterior to the cephalic capsule in the male which do not occur in the female. The tail is fairly short and stout in

both sexes (Text-fig. 108). In the male the spicules are simple and needle-like with sharp distal ends and without alae. The gubernaculum is small and lies close to the spicules. There is a simple pre-cloacal supplement and a series of long stoutish ventro-lateral setae running on both sides of the body between the cloacal opening and the supplement.

DISCUSSION

The present species differs from the previously described males in the possession of long, thin spicules—they are relatively short and stout in the two known species. It also differs from *T. galeata* and *T. longissima* in the amphids not lying posterior to the cephalic capsule. Filipjev (1927) in his treatment of this genus refers to the amphids of *T. barbata* as lying “Au milieu de la capsule céph.” but this is an error since Ditlevsen specifically says “Lateral organs (= amphids) are not seen in my specimen”. Ditlevsen does, however, refer to “In the very front-end of the body the spear is supported by short chitinous rods . . .” which are probably the mandibles. *T. barbata* was described from one “scarcely mature female . . .” and its status must be considered uncertain. The present species appears to differ from it in having relatively shorter cephalic setae.

Enoplus Dujardin, 1845

This genus, the type of the family, is one of the most easily recognized among the marine members of the Order. The reduction and concentration of the mandibular and onchial complexes to form one massive median organ in each lip is so spectacular that there is no difficulty in identifying its members. Two species are present in the collections, one of which is new and the other previously described.

Enoplus harlockae sp. nov.

(Text-figs. 110, 113, 115)

MATERIAL STUDIED. 1 ♂ (holotype), 1 ♀, 1 larva. 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 130–132.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Male	28.0	5.5	16.8		4.2
Female	25.6	5.6	14.1	56.1	4.1
Larva	23.3	4.7	13.3		2.8

MEASUREMENTS (in mm.). *Male*. Body breadth : 0.15. Oesophagus length : 0.76. Length of cephalic setae, long/short : 0.020/0.018. Diameter of cephalic capsule at posterior edge : 0.066. Distance of eye spots from anterior end of body : 0.069. Length of mandibles : 0.026. Distance of nerve ring from anterior end of body : 0.32. Distance of excretory pore from anterior end of body : 0.25. Tail length : 0.25. Cloacal diameter : 0.12. Spicule length : 0.144. Gubernaculum length : 0.069. Pre-cloacal supplement, length/distance anterior to cloacal opening : 0.099/0.24.

Female. Body breadth : 0.16. Oesophagus length : 0.73. Length of cephalic setae, long/short : 0.018/0.013. Diameter of cephalic capsule at posterior edge : 0.069. Distance of eye spots from anterior end of body : 0.069. Length of mandibles : 0.026. Distance of nerve ring from anterior end of body : 0.33. Distance of excretory pore from anterior end of body : 0.26. Tail length : 0.29. Anal diameter : 0.11. Distance of vulva from anterior end of body : 2.3. Size of egg : 0.096×0.126 .

Larva. Body breadth : 0.12. Oesophagus length : 0.60. Length of cephalic setae, long/short : 0.018/0.015. Diameter of cephalic capsule at posterior edge : 0.051. Distance of eye spots from anterior end of body : 0.051. Length of mandibles : 0.021. Distance of nerve ring from anterior end of body : 0.27. Distance of excretory pore from anterior end of body : 0.22. Tail length : 0.21. Anal diameter : 0.084.

The amphids lie on the posterior edge of the cephalic capsule (Text-fig. 111) and the head is otherwise typical (see page 282). The tail is fairly short and stout with a short, narrow terminal part (Text-fig. 115) in both sexes.

In the male the spicules are stout and S-shaped with two large barb-like plates and apparently very narrow alae (Text-fig. 113). The gubernaculum is short and the median and the lateral pieces curve upwards to enfold the spicules (Text-fig. 113). The pre-cloacal supplement is straight and swollen at its proximal end and the distal end is divided into three hook-like processes (this appears to be common in the supplement of *Enoplus* species although it seems to have been mentioned only by Mawson (1958) in *E. michaelsoni*). There are the usual long, stout setae on the ventro-lateral surfaces of the body between the cloacal opening and the pre-cloacal supplement (Text-fig. 115).

DISCUSSION

This species is most similar in general appearance to *E. meridionalis* Steiner, 1922 but is characterized by the form of the pre-cloacal supplement, the short, S-shaped spicules with only two plates and the shape of the gubernaculum, which appears to be unique. The position of this latter structure is unlikely to be due to muscle contraction because of the relationships between the side pieces and the median joining piece.

Enoplus michaelsoni Linstow, 1896

MATERIAL STUDIED. 1 ♂, 1 larvae. 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. No. 1963. 137-138.

Ratios			
<i>a</i>	<i>b</i>	<i>c</i>	Body Length (male) (mm.)
44.4	8.3	27.3	6.0

MEASUREMENTS (in mm.). *Male.* Body breadth : 0.14. Oesophagus length : 0.72. Length of cephalic setae, long/short : 0.023/0.015. Diameter of cephalic capsule at posterior end : 0.075. Distance of eye spots from anterior end of body : 0.081.

Distance of nerve ring from anterior end of body : 0.33. Distance of excretory pore from anterior end of body : 0.25. Length of mandibles : 0.033. Tail length : 0.22. Cloacal diameter : 0.096. Spicule length : 0.144. Gubernaculum length : 0.075. Pre-cloacal supplement, length/distance anterior to cloacal opening : 0.075/0.19.

This species is typical of the genus and is characterized by the amphids lying anterior to the posterior edge of the cephalic capsule (Text-fig. 112), the large trumpet-shaped pre-cloacal supplement and the form of the spicules and gubernaculum (Text-fig. 114). De Man's (1904) figures of this species are particularly good and I differ from him only in finding a ventral spine on the distal ends of the gubernaculum. The spicules bear five large plates close together and a small more distal one.

Rhabdodemanina Baylis and Daubney, 1926

As Filipjev (1934) points out this is a very distinctive genus for which he creates a new subfamily. However, as Wieser (1959) suggests, the buccal cavity may be interpreted as composed of three modified mandibles (see above, page 282) but this does not simplify the relationships of the genus which is still very different from the typical Enoplidae facies. The onchial cavity has expanded until it dominates the anterior end of the body, the cephalic capsule appears to be lost and the buccal cavity is reduced to a shallow space. The genus is probably near the Enchilidiinae/Eurystomatinae group but, provisionally, I shall refer it to the family Enoplidae.

Rhabdodemanina nancyae sp. nov.

(Text-figs. 116-120)

MATERIAL STUDIED. 10 + ♂♂, 10 + ♀♀. 35° 58.8' S./25° 42.2' E. on 24.11.60 from coarse sand and broken shells at a depth of 26 metres (SCD 212). B.M. (N.H.), Reg. Nos 1963. 299-318.

3 ♂♂, 5 ♀♀, 4 larva. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 93 (returned to South Africa).

6 ♂♂, 8 ♀♀, 3 larvae. 35° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 319-335.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	51.3	6.8	20.6		3.7
	46.9	6.9	22.4		3.8
	48.1	7.1	21.7		3.9
Females	48.7	7.0	23.1	59.5	3.7
	49.4	7.2	21.1	60.5	3.8
	45.9	7.0	20.5	56.4	3.9

MEASUREMENTS (in mm., in order of body lengths above). *Males*. Body breadth : 0.072 ; 0.081 ; 0.081. Oesophagus length : 0.54 ; 0.55 ; 0.55. Diameter of head : 0.014 ; 0.014 ; 0.016. Depth of buccal cavity : 0.017 ;

0.016 ; 0.018. Width of buccal cavity : 0.008 ; 0.009 ; 0.011. Length of cephalic setae, long/short : 0.011/0.006 ; 0.012/0.007 ; 0.012/0.007. Distance of nerve ring from anterior end of body : 0.21 ; 0.25 ; 0.26. Distance of excretory pore from anterior end of body : 0.022 ; 0.024 ; 0.025. Tail length : 0.18 ; 0.17 ; 0.18. Cloacal diameter : 0.058 ; 0.058 ; 0.058. Length of spicules : 0.051 ; 0.058 ; 0.053. Length of gubernaculum : 0.029 ; 0.032 ; 0.035.

Females. Body breadth : 0.076 ; 0.071 ; 0.085. Oesophagus length : 0.53 ; 0.53 ; 0.56. Diameter of head : 0.013 ; 0.013 ; 0.015. Depth of buccal cavity : 0.018 ; 0.017 ; 0.019. Width of buccal cavity : 0.008 ; 0.010 ; 0.011. Distance of nerve ring from anterior end of body : 0.23 ; 0.24 ; 0.26. Distance of excretory pore from anterior end of body : 0.020 ; 0.023 ; 0.024. Tail length : 0.16 ; 0.18 ; 0.19. Anal diameter : 0.054 ; 0.057 ; 0.058. Distance of vulva from anterior end of body : 2.2 ; 2.3 ; 2.2.

The mouth opening appears to be large and circular but it is very difficult to be sure because of the size and condition of the specimens but the lining of the mouth opening is striated (Text-figs. 117 and 121). Wieser (1959) refers to "... strongly developed, cushion-like " lips but he is clearly only referring to the stout projecting anterior end of the body. A very poorly developed cephalic capsule appears to be present but this, also, is uncertain. The oesophagus expands evenly along its length and is cellular posteriorly. There is a large dorsal onchium and two small, equal ventro-lateral onchia. The tail is stout and blunt posteriorly and the three caudal glands lie posterior to the cloacal opening (Text-fig. 120).

The spicules are of the form typical for the genus, equal in length and identical in structure with rather square distal ends. The gubernaculum is slim and lightly built and there is no pre-cloacal supplement (Text-fig. 119). There is only one testis.

The reproductive system is double with opposed uteri and reflexed ovaries. The oviducts are modified as spermathecae and the eggs are relatively very large, 0.189 mm. \times 0.045 mm. and 0.200 mm. \times 0.048 mm. for example.

DISCUSSION

The species described above is clearly distinct from the five species currently referred to the genus. It differs from *R. major* (Southern, 1914), *R. coronata* Gerlach, 1952 and *R. illgi* Wieser, 1959 in having the cephalic setae arranged in one circle and not two. It appears to differ from the two remaining species, *R. minor* (Southern, 1914) and *R. gracilis* (Ditlevsen, 1919), in the form of the spicules but I am not sure how reliable this character is although Filipjev (1927) stresses it in considering *R. minor* and *R. gracilis*. *R. nancyae* is, however, easily distinguished from all the previous species by the small size of the ventro-lateral onchia which, compared with the dorsal onchium, are almost wholly reduced.

R. nancyae is characterized by cephalic setae in one circle, square-ended spicules and greatly reduced ventro-lateral onchia.

Family **LEPTOSOMATIDAE** Filipjev, 1916

This family is quite distinct from the Enoplidae and Phanodermatidae in the structure of the head and the form of the oesophagus. There are, however, two distinct groups within it as at present constituted. As Mawson (1956) rightly points out, keys to the Leptosomatidae tend to divorce *Thoracostoma* from *Leptosomatum* to which it shows clear affinities. *Leptosomatum* Bastian, 1865, *Leptosomatides* Filipjev, 1918, *Paraleptosomatides* Mawson, 1956, *Corythostoma* Wieser, 1956, *Synonchoides* Wieser, 1956 and *Thoracostoma* Marion, 1870 clearly form a distinctive group on the form of the tail, the spicules, and also the structure of the head. Wieser (1956) proposes *Corythosoma* and *Synonoides* as subgenera of *Thoracostoma* but there is more reason to consider them distinct genera than there is for treating *Paraleptosomatides*, for example, as a distinct genus. The genera *Macronchus* gen. nov., *Jagerskioldia* Filipjev, 1916, *Synonchus* Cobb, 1894, *Cylicolaimus* de Man 1889a and *Platycoma* Cobb, 1893 form another group with which *Barbonema* Filipjev, 1927 and *Parabarbonema* gen. nov. should probably be associated. Possibly *Platycomopsis* Ditlevsen, 1926 and *Metacylicolaimus* Schuurmans Stekhoven, 1946 also belong with this group. The genera *Anticoma* Bastian, 1865, and *Paranticoma* Micoletzky, 1930 are the only forms in the family in which the pre-cloacal supplement is rod-like but this I interpret as a primitive character and would not consider it any reason to transfer these two genera from the family. The most that can safely be said about this family is that there are two different groups of highly evolved genera, the first and second adumbrated above, but as the information on so many of the others is insufficient the family is best left as one major undivided group. It may be diagnosed as follows :

Enoplida : posterior part of oesophagus never showing "cellular" appearance ; amphids pocket-like ; buccal cavity never large ; onchia carried far forward and supplied by muscles passing through cephalic vesicle ; pre-cloacal supplements generally papilloid, if not, then simple rod-like ; spicules never very complex with plates ; cephalic capsule in highly evolved forms very prominent ; cephalic ring not prominent.

TYPE GENUS : *Leptosomatum* Bastian, 1865.

Anticoma Bastian, 1865

This genus is usually defined as lacking a cephalic capsule and onchia but in fact several species with both these features have previously been referred to the genus. The species I describe below is so equipped but I prefer to refer it to *Anticoma* rather than attempt to untangle the genus as at present constituted.

Anticoma chitwoodi sp. nov.

(Text-figs. 122-131)

MATERIAL STUDIED. 2 ♂♂ (1 selected as holotype), 1 ♀. 34° 02'S./23° 48'4"E. on 29.II.60 from sand, mud and rock at a depth of 50 metres (SCD 220). B.M. (N.H.), Reg. Nos. 1963. 42-44.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	48.8	5.9	7.5		4.0
	51.8	5.5	7.7		4.3
Female	47.4	6.4	7.9	43.5	4.6

MEASUREMENTS (in mm., in order of body lengths above). *Males*. Body breadth : 0.082 ; 0.083. Oesophagus length : 0.68 ; 0.78. Cephalic capsule, depth/diameter at posterior edge : 0.013/0.021 ; 0.012/0.018. Length of cephalic setae, long/short : 0.018/0.011 ; 0.017/0.011. Distance of cervical setae from anterior end of body : 0.054 ; 0.047. Distance of nerve ring from anterior end of body : 0.29 ; 0.32. Distance of excretory pore from anterior end of body : 0.19 ; 0.23. Tail length : 0.53 ; 0.56. Cloacal diameter : 0.053 ; 0.069. Spicule length : 0.084 ; 0.099. Gubernaculum length : 0.032 ; 0.036. Length of pre-cloacal supplement : 0.017 ; 0.015. Distance of pre-cloacal supplement anterior to cloacal opening : 0.078 ; 0.072.

Female. Body breadth : 0.097. Oesophagus length : 0.72. Cephalic capsule, depth/diameter at posterior edge : 0.011/0.024. Length of cephalic setae, long/short : 0.018/0.012. Distance of cervical setae from anterior end of body : 0.056. Distance of nerve ring from anterior end of body : 0.31. Distance of excretory pore from anterior end of body : 0.22. Tail length : 0.58. Anal diameter : 0.052. Distance of vulva from anterior end of body : 2.0. The eggs are 0.189 mm. \times 0.073 mm.

The head is rounded in outline with a distinct cephalic capsule on the posterior edge of which lie the openings of the amphids (Text-fig. 126). The capsule in one male specimen is fenestrate, as is shown in Text-figs. 126-131. The anterior end of each sector of the oesophagus carries a small onchium which arises from a thickening of the cuticular covering of the oesophagus (Text-figs. 122 and 125). The cervical setae vary from three to five in number.

The tail in both sexes narrows rapidly to end in a very long terminal filament (Text-fig. 124). In the male the spicules are lightly built with wide alae and the gubernaculum is fairly long with prominent lateral pieces which are blunt posteriorly (Text-fig. 123). The pre-cloacal supplement is rod-like and two rows of stout setae are carried on the ventro-lateral aspects of the body between the supplement and the cloacal opening (Text-fig. 124).

DISCUSSION

The cephalic capsule appears to be more strongly developed than is usually the case but I am not sure that this is a good character as it was best seen in uncleared specimens. However, even in those cleared with glycerine, its presence could easily be established. The species is distinct from all others in the form of the lightly built spicules, the structure of the gubernaculum, the great length of the tail, the presence of distinct onchia at the anterior end of the oesophagus and the position of the excretory pore. *A. chitwoodi* appears to be most similar to *A. columba* Wieser, 1953—which is also reported from a subantarctic locality,

MacRobertson Land by Mawson (1958a)—but differs in the extreme length of the tail, the more anterior position of the amphid, the less prominent pre-cloacal supplement (probably an unreliable character), the structure of the spicules and gubernaculum. It is also similar to *A. kerguelensis* Mawson, 1958a from which it differs in the more massive gubernaculum, the form of the spicules and the prominent amphids which lie relatively farther anterior in position.

PARABARBONEMA gen. nov.

The species I describe below was at first considered to belong to the genus *Barbonema* Filipjev, 1927 but it is clear that a new genus is required for its reception. Filipjev (1927) describes the spicules in *B. setifera* Filipjev, 1927 as apparently incompletely developed while Gerlach (1956) in describing his new species, *B. horridum*, is unable to decide whether there are two or only one spicule present and later, in describing *B. flagrum* Gerlach, 1957, makes the same comment. The spicules and gubernaculum in the species described below are very similar to those described by Filipjev and Gerlach but these authors are agreed that there is no pre-cloacal supplement in any of their species and the tail is long with a semi-flagellate end. In all three the amphids lie posterior to the longest post-cephalic setae (although in the case of *B. flagrum* this is a little uncertain) while in the present species they lie anterior to them and in all three the labial sense organs are (?) setose while in this species they are not. In view of this combination of a short tail, a pre-cloacal supplement, the position of the amphids on the posterior edge of the cephalic capsule and the form of the labial sense organs I propose to refer this species to a new genus, *Parabarbonema*. It may be pointed out here that *B. flagrum* appears to be very different from the other two species referred to *Barbonema* and will probably warrant separation in a distinct genus when more species are known. The new genus *Parabarbonema* may be diagnosed thus :

Leptosomatidae : cephalic capsule well developed, unlobed ; labial sense organs papillate ; anterior ends of oesophageal sectors modified as broad onchia ; amphids prominent, opening on posterior edge of cephalic capsule ; all long cervical setae posterior to amphids ; tail short and stout in both sexes.

MALE : papillate pre-cloacal supplement present ; spicules short and stout ; gubernaculum large, indistinct, with large thin sheets of cuticle enfolding spicules.

TYPE SPECIES : *Parabarbonema barba* sp. nov.

Parabarbonema barba sp. nov.

(Text-figs. 32-137)

MATERIAL STUDIED. 12 ♂♂ (1 selected as holotype), 17 ♀♀, 29 larvae. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 202-259.

2 ♂♂ (+ 1 ♂ in very poor condition). 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres. WCD 94 (returned to South Africa).

6 ♂♂, 3 ♀♀, 3 larvae. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand from a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 260-271.

	Ratios			V	Body Length (mm.)
	a	b	c		
Males	96.0	6.3	53.3		9.6
	98.0	7.1	57.6		9.8
	108.9	7.5	70.0		9.8
	97.3	8.4	62.9		10.7
Females	93.0	6.3	42.3	71.0	9.3
	99.1	7.6	49.5	63.6	10.9
Larva	91.7	7.8	53.1		10.1

MEASUREMENTS (in mm. in order of body lengths above). *Males*. Body breadth : 0.10 ; 0.099 ; 0.091 ; 0.11. Oesophagus length : 1.52 ; 1.37 ; 1.30 ; 1.28. Diameter of head : 0.027 ; 0.029 ; 0.025 ; 0.024. Diameter of cephalic capsule at posterior end : 0.030 ; 0.031 ; 0.029 ; 0.028. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0.019 ; 0.021 ; 0.017 ; 0.016. Length of cephalic setae : 0.029 ; 0.029 ; 0.024 ; 0.024. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0.029/0.022 ; 0.028/0.023 ; 0.023/0.020 ; 0.024/0.022. Distance of nerve ring from anterior end of body : 0.41 ; 0.47 ; 0.43 ; 0.43. Distance of excretory pore from the anterior end could be measured only in the 10.7 mm. long specimen where it is 0.12. Tail length : 0.18 ; 0.17 ; 0.14 ; 0.17. Cloacal diameter : 0.08 ; 0.08 ; 0.08 ; 0.09. Spicule length : 0.082 ; 0.079 ; 0.063 ; 0.084. Distance of pre-cloacal supplement anterior to cloacal opening : 0.12 ; 0.098 ; 0.090 ; 0.11.

Females. Body breadth : 0.099 ; 0.11. Oesophagus length : 1.48 ; 1.43. Diameter of head : 0.020 ; 0.028. Diameter of cephalic capsule at posterior end : 0.036 ; 0.034. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0.022 ; 0.020. Length of cephalic setae : 0.027 ; 0.029. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0.026/0.026 ; 0.028/0.026. Distance of nerve ring from anterior end of body : 0.043 ; 0.046. Excretory pore not seen. Tail length : 0.22 ; 0.22. Anal diameter : 0.09 ; 0.08. Distance of vulva from anterior end of body : 6.6 ; 7.0.

Larva. Body breadth : 0.11. Oesophagus length : 1.37. Diameter of head : 0.028. Diameter of cephalic capsule at posterior end : 0.020. Distance of amphid from anterior end of body (= depth of cephalic capsule) : 0.019. Length of cephalic setae : 0.028. Length of cervical setae, long pair immediately posterior to amphid/shorter setae scattered posterior to paired setae : 0.027/0.023. Distance of nerve ring from anterior end of body : 0.39. Excretory pore not seen. Tail length : 0.19. Anal diameter : 0.08.

The head bears the usual ten long setae and an inner circle of six papillae. The long setae are about the same length and I have been unable to distinguish between sets of long and short (Text-figs. 132 and 133). The cephalic capsule is simple but

distinct and the openings of the large pocket amphids lie on the posterior edge of the capsule (Text-fig. 133). Immediately posterior to the amphids lie two long, equal setae which arise very close together. These setae are long, about the same length as the cephalic setae (see measurements above), and are followed by a series of shorter setae on the anterior part of the body. These body setae occur in eight files over roughly the anterior seventh of the length of the oesophagus becoming smaller and further apart posteriorly. The oesophagus is non-muscular, without any posterior swelling but with a well developed oesophageal-intestinal valve.

The tail is short and stout in both sexes and ends in a blunt, rounded tip (Text-fig. 134). In the male there is a papillate pre-cloacal supplement similar to that occurring in the genus *Thoracostoma*. A series of ventro-lateral, stout setae occur on the tail and on the body between the cloacal opening and the supplement. The spicules are equal and identical and are bluntly rounded posteriorly. The gubernaculum is in two parts and is developed as an extensive, thin sheet round both spicules. This sheet arises from well developed lateral portions—lying dorsal to the spicules—which are modified distally as relatively massive, apparently slightly toothed, regions which are rather similar in appearance to the distal ends of the gubernaculum in species of *Cyatholaimus* (Text-figs. 135 and 136).

***MACRONCHUS* gen. nov.**

One species which is present in the collection in very large numbers is most similar to those referred to the genus *Synonchus* in particular and the genera *Jager-skioldia* and *Cylicolaimus* in general but differs from them in possessing two pre-cloacal supplements, very massive spicules, a massive dentate distal end to the gubernaculum and large onchia developed from the centre of each sector of the oesophagus. It is very distinctive and I propose to refer it to a new genus, *Macronchus*.

LEPTOSOMATIDAE : cephalic capsule narrow ; large median onchia on each sector of oesophagus ; small wholly cuticular odontia developed from lining of buccal cavity.

MALE : two pre-cloacal supplements, more anterior large and double, more posterior single and papillate ; body swollen anterior to cloacal opening, bearing long stout setae in several rows ventro-laterally ; gubernaculum with massive dentate distal ends.

TYPE SPECIES : *Macronchus shealsi* sp. nov.

***Macronchus shealsi* sp. nov.**

(Text-figs. 138-147)

MATERIAL STUDIED. 13 ♂♂ (1 selected as holotype), 11 ♀♀, 9 larvae. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 90). B.M. (N.H.), Reg. Nos. 1963. 59-91.

11 ♂♂, 12 ♀♀, 8 larvae. 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 93-123.

5 ♂♂. 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 102). B.M. (N.H.), Reg. Nos. 1963. 124-128.

1 larva. 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.) Reg. No. 1963. 92.

15 ♂♂, 18 ♀♀, 22 larvae. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres. WCD 93 (returned to South Africa).

	Ratios				Body Length
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	(mm.)
Males	50.0	6.4	25.0		11.0
	53.2	6.8	25.4		11.7
	56.7	7.1	29.0		11.9
	55.9	6.9	25.6		12.3
Females	57.1	7.1	27.9	46.5	12.0
	56.8	7.6	27.2	48.9	12.5
	60.0	7.0	26.4	53.8	13.2
Larvae (4th stage ♀)	52.4	7.0	25.6	49.1	11.0
	53.0	7.5	26.5	49.2	12.2

MEASUREMENTS (in mm., in order of body lengths above). *Males*. Body breadth : 0.22 ; 0.22 ; 0.21 ; 0.22. Oesophagus length : 1.72 ; 1.71 ; 1.68 ; 1.77. Diameter of head : 0.054 ; 0.049 ; 0.041 ; 0.057. Length of cephalic setae, long/short : 0.014/0.013 ; 0.014/0.013 ; 0.014/0.012 ; 0.015/0.013. Distance of nerve ring from anterior end of body : 0.49 ; 0.49 ; 0.46 ; 0.51. Tail length : 0.44 ; 0.41 ; 0.41 ; 0.48. Cloacal diameter : 0.192 ; 0.176 ; 0.168 ; 0.188. Spicule length : 0.216 ; 0.214 ; 0.192 ; 0.219. Gubernaculum length : 0.099 ; 0.098 ; 0.096 ; 0.102. Distance of first pre-cloacal supplement anterior to cloacal opening : 0.210 ; 0.206 ; 0.195 ; 0.214. Distance of second (i.e. more anterior) pre-cloacal supplement anterior to cloacal opening : 0.47 ; 0.47 ; 0.44 ; 0.47.

Females. Body breadth : 0.21 ; 0.22 ; 0.22. Oesophagus length : 1.69 ; 1.64 ; 1.86. Diameter of head : 0.054 ; 0.052 ; 0.059. Length of cephalic setae, long/short : 0.014/0.013 ; 0.013/0.012 ; 0.013/0.012. Distance of nerve ring from anterior end of body : 0.47 ; 0.47 ; 0.48. Tail length : 0.43 ; 0.46 ; 0.50. Anal diameter : 0.12 ; 0.13 ; 0.14. Distance of vulva from anterior end of body : 5.6 ; 6.1 ; 6.9.

Larvae. Body breadth : 0.21 ; 0.23. Oesophagus length : 1.56 ; 1.62. Diameter of head : 0.061 ; 0.066. Length of cephalic setae, long/short : 0.014/0.012 ; 0.014/0.013. Distance of nerve ring from anterior end of body : 0.47 ; 0.52. Tail length : 0.43 ; 0.46. Anal diameter : 0.14 ; 0.13. Distance of vulva from anterior end of body : 5.4 ; 6.0.

The head is bluntly rounded with a narrow cephalic capsule. There is an inner circle of six sessile papillae and an outer circle of ten setae of which six are longer than the remaining four (Text-fig. 143). The median onchium on each lip is large, prominent and the same size on all three lips. The small amphids lie posterior to the cephalic capsule. There is a series of setae on the anterior part of the body posterior to the head (Text-fig. 142) arranged in distinct groups. A series of wholly cuticular teeth arise from the cuticular lining of the buccal cavity (Text-figs. 138,

139 and 141). The head is relatively large, i.e. the body does not narrow markedly anteriorly. The oesophagus is not muscular posteriorly. The ventro-lateral oesophageal glands open at the bases of the large onchia while the dorsal gland duct opens through a small denticle-like structure some distance posterior to the large median onchium (Text-fig. 141).

The tail is stout in both sexes with a narrow terminal zone (Text-fig. 145). In the male there is a definite ventral bump immediately anterior to the beginning of this narrow zone which is due to a thickening of the cuticle. The male tail is further characterized by the presence of two pre-cloacal supplementary structures (Text-figs. 145 and 147). Of these the more anterior is the larger and consists of a raised area of cuticle, supplied by special musculature, in which are two slightly curved rows of small rods pierced by channels (Text-fig. 144). The more posterior supplement is more papillate in appearance but when studied from the ventral aspect is supported by a thickening of the cuticle as shown in Text-fig. 147. The body immediately anterior to the cloacal opening is markedly wider than at any other point on the body (see Text-fig. 147) and this area is covered on each ventro-lateral area by a series of long, stout setae. The most lateral setae are the longest and stoutest and become increasingly smaller and slimmer towards the ventral surface. The spicules are equal, identical and massive (Text-figs. 146 and 147) with narrow alae. Note that the outer part of the spicule along the non-alate side is much thicker than along the alate surface. The gubernaculum is relatively small in two parts with distinctly toothed, relatively massive distal heads (Text-figs. 146 and 147).

Thoracostoma Marion, 1870

This genus is with *Enoplus* one of the most easily recognized in any sample because of the massive development of the cephalic capsule. This has had a disadvantageous effect on the taxonomy of the group since the shape of the capsule and the distribution and shape of the various locules which are frequently present have been used to delimit a large number of species. Filipjev (1916) and Wieser (1953) both report specimens, otherwise typical *T. articum*, in which no locules are present and Mawson (1956) points out that "the exact shape, and the number of loculi, are often subject to individual variation". However no-one has previously studied the variation in the form of the locules in the entire capsule in a number of specimens, although Mawson (1958a) gives a dorsal, ventral and lateral view for the species she describes. I have studied the form of the posterior part of the capsule in detail in the three species I describe below, and its structure is illustrated in Text-figs. 148, 159-162, 163-166 and 177-179. Each figure represents the capsule of one specimen with the dorsal lobe in the centre, the right dorso-lateral, the right ventro-lateral and the ventral lobes drawn to the right and the left dorso-lateral, the left ventro-lateral and the ventral lobes drawn to the left. That is, the ventral lobe is shown twice, on the extreme right and left of the strip. Each figure represents a compilation from twelve separate figures—one for each sector of the capsule and one for each incision. The distribution of the nuchal setae is also shown. One

thing is immediately obvious from the figures, there is no sexual dimorphism. Secondly, the number of locules is of no value nor is their detailed shape. These factors vary too much, but certain conclusions can be drawn. The locules are simpler in the larvae and their size and number tends to increase in the adults. This increase in size, to the point where the locules fuse, is most spectacular in *T. zeae* (Text-figs. 177–179) but the same tendency is seen in *T. jae* (Text-figs. 159–166). The locules seem to follow a fairly definite pattern in the two species considered in detail here but I suspect that this would be of very little value if more species were taken into consideration. Nevertheless, the capsule has a characteristic appearance in all three species. This is largely a reflection of the length of the capsule from the anterior edges of the lacunae to the posterior edge of the capsule, the shape of the fenestrae and the width of the incisions. The distribution of the nuchal setae is also probably of some value but only those on the lateral aspect where they tend to occur in groups just posterior to the amphidial incision. I suspect that this also will break down when a wide range of species has been studied. The best characters still appear to be those afforded by the buccal armature—probably at a generic level—while the form of the male reproductive apparatus supplies very valuable characters for the delimitation of species. While the argument that characters are most useful when they allow both sexes to be separated has some validity it is unfortunately true that in many groups of nematodes it is extremely difficult, if not impossible, to separate females and the form of the gubernaculum in this genus appears to be particularly valuable in separating males. Many of the figures which have been published of the spicules and gubernaculum are quite insufficient by any standards and the real value of the variation of this set of organs cannot at present be assessed. In future descriptions attention must be paid not only to the form of the buccal armature—as has been stressed by Wieser (1956) and Mawson (1958a)—but also to the structure of the gubernaculum, in particular, and spicules. The importance of the presence or absence of a distal spine on the gubernaculum is uncertain since it appears either to vary in its occurrence or to be extremely difficult to find in some specimens and I would not recognize its absence as being of any significance.

***Thoracostoma angustifissulatum* Mawson, 1956**
(Text-figs. 148–151)

MATERIAL STUDIED. 1 ♂. 32° 16' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. No. 1963. 21.

a	Ratios		Body Length (mm.)
	b	c	
42.9	5.1	69.8	9.0

MEASUREMENTS (in mm.). Body breadth : 0.21. Oesophagus length : 1.76. Cephalic capsule, depth/diameter at posterior edge : 0.042/0.060. Distance of nerve ring from anterior end of body : 0.54. Distance of eye spots from anterior end of body : 0.159. Tail length : 0.129. Cloacal diameter : 0.186. Spicule length :

0.213. Gubernaculum length : 0.148. Distance of pre-cloacal supplement anterior to cloacal opening : 0.114.

The head is exactly as described by Mawson (1956) which is the same as that of *T. jae* (see page 333). The posterior edge of the capsule is somewhat incised and the lacunae pierce each lobe relatively far anterior to the posterior edge of the capsule, roughly half-way between that edge and the level of the cephalic setae (Text-fig. 148). This also is stressed by Mawson. I have been unable to see any nuchal setae but Mawson points out that they are small and sparse in her specimens. There are paired eye spots with lenses.

The tail is very short and stout with the papillate pre-cloacal supplement lying relatively close to the cloacal opening. Anterior to the supplement are five pairs of papillae. The spicules are massive terminating distally in sharpish points. The gubernaculum is large with a distal process and a massive rounded proximal end. The distal end of the gubernaculum is blunt (Text-fig. 151).

DISCUSSION

Mawson records this species from many Arctic and Subantarctic localities. For details reference should be made to the original publications, Mawson : 1956, 1958, 1958a. The species is characterized by the form of the mouth armature, the length of the cephalic capsule, the occurrence of the lacunae of the capsule relatively far anterior to the posterior edge, and the massive form of the gubernaculum.

Thoracostoma jae sp. nov.

(Text-figs. 152-166)

MATERIAL STUDIED. 6 ♂♂ (1 selected as holotype), 5 ♀♀, 5 larvae. 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 166-179 (1 ♂, 1 ♀ returned to South Africa).

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	35.4	5.1	65.8		6.7
	35.5	5.0	69.8		7.1
	31.3	4.9	61.5		7.2
	38.0	5.3	74.3		7.6
	39.5	5.7	79.0		8.3
	44.0	5.4	76.5		8.8
Females	29.6	5.0	79.6	66.2	7.4 (? 4th-larva)
	33.7	5.5	79.2	62.0	8.4
	34.6	5.7	78.9	64.4	9.0
	40.0	5.5	82.1	61.9	9.2
	42.8	5.7	83.2	62.8	9.4
	23.3	3.6	48.6		3.5
Larvae	34.6	4.0	47.0		3.8
	30.0	5.3	74.2		6.9

MEASUREMENTS (in mm. in order of body lengths above). *Males*. Body breadth : 0.19 ; 0.20 ; 0.23 ; 0.20 ; 0.21 ; 0.20. Oesophagus length : 1.33 ; 1.43 ; 1.46 ;

1.44; 1.46; 1.62. Cephalic capsule, depth/diameter at posterior edge: 0.032/0.058; 0.039/0.060; 0.036/0.060; 0.039/0.057; 0.036/0.057; 0.039/0.057. Distance of nerve ring from anterior edge of body: 0.43; 0.45; 0.47; 0.47; 0.49; 0.50. Distance of eye spots from anterior end of body: 0.126; 0.138; 0.132; 0.120; 0.123; 0.132. Tail length: 0.102; 0.102; 0.117; 0.102; 0.105; 0.114. Cloacal diameter: 0.116; 0.120; 0.141; 0.138; 0.156; 0.132. Spicule length: 0.149; 0.165; 0.153; 0.162; 0.156; 0.144. Gubernaculum length: 0.113; 0.119; 0.112; 0.122; 0.116; 0.114. Distance of pre-cloacal supplement anterior to cloacal opening: 0.099; 0.121; 0.109; 0.097; 0.111; 0.120. Number of pairs of ventro-lateral papillae anterior to pre-cloacal supplement: 6, 6, 5, 7, 6, 5.

Females. Body breadth: 0.25; 0.25; 0.26; 0.23; 0.22. Oesophagus length: 1.48; 1.53; 1.57; 1.68; 1.66. Cephalic capsule, depth/diameter at posterior edge: 0.029/0.057; 0.033/0.057; 0.042/0.063; 0.048/0.063; 0.049/0.061. Distance of nerve ring from anterior end of body: 0.49; 0.48; 0.50; 0.54; 0.49. Distance of eye spots from anterior end of body: 0.126; 0.138; 0.135; 0.132; 0.129. Tail length: 0.093; 0.106; 0.114; 0.112; 0.113. Anal diameter: 0.112; 0.120; 0.134; 0.120; 0.131. Distance of vulva from anterior end of body: 4.9; 5.2; 5.8; 5.7; 5.9. The eggs are 0.387×0.150 ; 0.344×0.174 ; 0.288×0.180 ; 0.393×0.138 .

Larvae. Body breadth: 0.15; 0.11; 0.23. Oesophagus length: 0.97; 0.95; 1.30. Cephalic capsule, depth/diameter at posterior end: 0.027/0.039; 0.033/0.045; 0.029/0.051. Distance of nerve ring from anterior end of body: 0.36; 0.35; 0.44. Distance of eye spots from anterior end of body: 0.099; 0.114; 0.123. Tail length: 0.072; 0.081; 0.093. Anal diameter: 0.078; 0.078; 0.114.

The head carries a bifid onchium on the dorsal side of the mouth cavity and two thinner but similar bifid-structures on each ventro-lateral side of the mouth cavity (Text-figs. 157 and 158). The cephalic capsule is relatively short with narrow incisions and an irregular posterior edge. The fenestration lies near the posterior edge of the capsule and when extensive takes the form of long narrow fenestrae or several small circular fenestrae (Text-figs. 159–166). The nuchal setae tend to form single files on the dorso- and ventro-lateral sectors and to occur in groups of five or six, followed by single files, posterior to the amphids.

The spicules are rather lightly built, the gubernaculum is slim and no distal lateral processes were seen (Text-fig. 155). There are five to seven pairs of papillae anterior to the pre-cloacal supplement the occurrence of which is detailed above. The testes are opposed.

DISCUSSION

This species appears to be, on the basis of the form of the cephalic capsule, close to *Thoracostoma antarcticum* (von Linstow, 1892) and, to a lesser extent, on the form of the spicules but differs from it in the lightly built gubernaculum—and the lighter build of the spicules. It is also similar to *T. steineri* Micoletzky, 1922 in the light

build of the spicules and gubernaculum but is totally different from it in the form of the cephalic capsule.

***Thoracostoma zeae* sp. nov.**

(Text-figs. 167-179)

MATERIAL STUDIED. 1 ♂ (holotype), 3 larvae. 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 133-136.

	Ratios			Body Length
	<i>a</i>	<i>b</i>	<i>c</i>	(mm.)
Male	32.5	6.6	74.3	10.4
Larvae	32.6	5.5	76.9	6.0
	40.5	5.6	76.0	7.3
	46.8	4.2	72.3	8.9

MEASUREMENTS (in mm. in order of body lengths above). *Male*. Body breadth : 0.32. Oesophagus length : 1.58. Cephalic capsule, depth/diameter at posterior edge : 0.030/0.066. Distance of nerve ring from anterior end of body : 0.51. Distance of eye spots from anterior end of body : 0.114. Tail length : 0.14. Cloacal diameter : 0.20. Spicule length : 0.28. Gubernaculum length : 0.18. Distance of pre-cloacal supplement anterior to cloacal opening : 0.13. Distance of first/second pair of papillae anterior to cloacal opening : 0.26/0.44.

Larvae. Body breadth : 0.19 ; 0.18 ; 0.19. Oesophagus length : 1.09 ; 1.30 ; 1.67. Cephalic capsule, depth/diameter at posterior edge : 0.027/0.048 ; 0.027/0.056 ; 0.027/0.060. Distance of nerve ring from anterior end of body : 0.354 ; 0.410 ; 0.396. Distance of eye spots from anterior end of body : 0.090 ; 0.090 ; 0.111. Tail length : 0.078 ; 0.096 ; 0.123. Anal diameter : 0.108 ; 0.129 ; 0.150.

The head has a large onchium in the centre of each ventro-lateral lobe of the mouth cavity but not on the dorsal (Text-fig. 171). The cephalic capsule is short with very wide incisions and a very irregular posterior edge. The fenestrations lie very near the posterior edge and on elaborating tend to increase in size and then to pierce the posterior edge (see Text-figs. 177-179). The nuchal setae are restricted to groups of four to six just posterior to the amphids. There are no long files of setae as in the other species described here. The frame-work of the amphids is very prominent and projects posteriorly as a square ended mass which occupies most of the space of the amphidial incisions. The eye spots are typical with prominent lens.

The male tail carries the usual median papilloid pre-cloacal supplement anterior to which are only two pairs of ventro-lateral papillae. Between the pre-cloacal supplement and the cloacal opening are a number of long ventro-lateral setae, with a series of short setae lying close together just anterior to the cloacal opening. The spicules are narrow proximally but broaden rapidly distal to the bend (Text-fig. 174 and 175). The gubernaculum is blunt both proximally and distally and is about the same width along its whole length. There is a stout lateral terminal process (Text-fig. 174).

DISCUSSION

This species is very distinctive in the massive breakdown of the cephalic capsule by the multiplication, extension and fusion of the lacunae and the form and position of the amphids. It is further characterized by, so far as it is possible to confirm this character, the form of the lip dentition, the presence of only two pairs of pre-cloacal papillae, the even thickness of the gubernaculum and, possibly, by the form of the spicules. It is perhaps most similar to *T. zolae* Marion, 1870 and *T. steineri* Micoletzky, 1922 but differs in the massive lacunation of the cephalic capsule, the form of the gubernaculum and in possessing only two pre-cloacal papillae. (See Schuurmans Stekhoven, 1943).

Family **ENCHILIDIIDAE** Micoletzky, 1924

Eurystomina Filipjev, 1918

This genus has been reviewed elsewhere and will not be discussed further here (Inglis, 1962).

Eurystomina sudensis sp. nov.

(Text-figs. 180-183)

MATERIAL STUDIED. 1 ♂ (holotype) and two very poorly preserved specimens, 1 ♂, 1 ♀. 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. No. 1963. 45.

Ratios			
<i>a</i>	<i>b</i>	<i>c</i>	Body Length (mm.)
186.0	6.9	62.9	8.1

MEASUREMENTS (mm.). Body breadth : 0.069. Oesophagus length : 1.17. Excretory pore immediately posterior to head. Cephalic setae, long/short : 0.019/0.005. Diameter of head : 0.034. Depth of buccal cavity : 0.030. Diameter of buccal cavity at level of denticles : 0.017. Length of longest tooth : 0.022. Tail length : 0.129. Cloacal diameter : 0.060. Spicule length : 0.066. Gubernaculum length : 0.034. Distance of 1st pre-cloacal supplement anterior to cloacal opening : 0.18. Distance of 2nd supplement anterior to first : 0.14.

This species is absolutely typical of the genus *Eurystomina* with the left ventro-lateral tooth the longest and with two rows of denticles in the mouth cavity except at the point opposite the longest onchium where there are three (Text-figs. 180 and 181). The spicules are short and fairly stout without dentate processes on the distal ends. The gubernaculum is simple and non-fenestrate with a small rounded apophysis (Text-fig. 182). The tail is short and stout (Text-fig. 183).

DISCUSSION

E. sudensis is characterized by the short, stout spicules, the short tail and the relatively small, simple gubernaculum.

Family **ONCHOLAIMIDAE** Micoletzky, 1922***Pontonema*** Leidy, 1855***Pontonema yaenae*** sp. nov.

(Text-figs. 184-188)

MATERIAL STUDIED. 10 ♂♂ (1 selected as holotype), 5 ♀♀, 3 larvae. 32° 02' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 91). B.M. (N.H.), Reg. Nos. 1963. 142-157. (1 ♂, 1 ♀ returned to South Africa).

2 ♂♂, 2 ♀♀ (+ 2 ♂♂, 1 ♀, 2 larvae in very poor condition). 32° 06' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 27 metres (WCD 99). B.M. (N.H.), Reg. Nos. 1963. 158-165.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	50.9	7.3	46.9		6.1
	58.2	7.1	45.7		6.4
Females	43.0	6.5	46.0	43.5	6.9
	41.8	6.8	41.7	47.9	7.1

MEASUREMENTS (in mm., in order of body lengths above). *Males*. Body breadth: 0.12; 0.11. Oesophagus length: 0.83; 0.91. Distance of nerve ring from anterior end of body: 0.36; 0.38. Distance of excretory pore from anterior end of body: 0.046; 0.048. Diameter of head: 0.054; 0.060. Length of cephalic setae, long/short: 0.014/0.010; 0.016/0.012. Buccal cavity, length/breadth: 0.093/0.036; 0.105/0.032. Tail length: 0.13; 0.14. Cloacal diameter: 0.064; 0.072. Length of spicules: 0.073; 0.072. Length of gubernaculum (= apophysis): 0.041; 0.048.

Females. Body breadth: 0.16; 0.17. Oesophagus length: 1.06; 1.04. Distance of nerve ring from anterior end of body: 0.41; 0.43. Distance of excretory pore from anterior end of body: 0.050; 0.052. Diameter of head: 0.063; 0.064. Length of cephalic setae, long/short: 0.012/0.011; 0.012/0.010. Buccal cavity; length/breadth: 0.114/0.039; 0.116/0.042. Tail length: 0.15; 0.17. Anal diameter: 0.075; 0.079. Distance of vulva from anterior end of body: 3.0; 3.4. Eggs are about 0.32 × 0.11 in size.

The head is typical with a large buccal cavity in which the dorsal onchium is smaller than the two equal ventro-lateral onchia and lies far posterior (Text-figs. 184 and 185). The amphids are prominent and the large semi-lunar openings lead into circular pouches (Text-fig. 185). There are several small setae on the body between the level of the amphids and the opening of the excretory pore which do not appear to follow a fixed pattern. The tail is short and stout in both sexes (Text-fig. 186).

The male tail bears a series of long, stout setae in two rows on the ventro-lateral surfaces and there is a similar series extending anteriorly from the cloacal opening. There are no pre-cloacal papillae. The spicules are simple in outline and the gubernaculum bears a distinct apophysis which is enlarged distally to enfold the spicules. This enlarged zone is pierced by a large circular hole (Text-fig. 188).

DISCUSSION

Kreis' (1934a) key has been modified and brought up to date by Mawson (1956) but I am not happy about keys based on ratios which lie as close together as, for example, Tail 1.5-2 \times anal breadth and Tail 1-1.5 \times anal breadth, particularly in a group such as this in which the tail tends to be strongly curled ventrally. If Mawson's key is used this species comes down to *Pontonema brevicaudatus* (Menzel, 1920) from which it differs markedly in lacking papillae on the male tail. It appears also to be similar in general appearance to *P. macrolaimus* (Southern, 1914), *P. parpapilliferus* Micoletzky, 1924 and *P. papilliferus* Filipjev, 1916 in the location of the dorsal onchium within the onchial cavity and the short tail but differs from all three species in the slim gubernaculum with its fenestrate distal end and in not possessing pre-cloacal papillae.

Family **IRONIDAE** de Man, 1876

Thalassironus de Man, 1889

Thalassironus jungi sp. nov.

(Text-figs. 189-194)

MATERIAL STUDIED. 3 ♂♂ (1 selected as holotype), 11 ♀♀, 5 larvae (mostly very coiled). 32° 05' S./18° 16' E. on 2.7.61 from khaki mud at a depth of 54 metres (WCD 94). B.M. (N.H.), Reg. Nos. 1963. 22-38. (1 ♂, 1 ♀ returned to South Africa).

2 ♂♂, 1 ♀. 32° 05' S./18° 17' E. on 2.7.61 from coarse white sand at a depth of 39 metres (WCD 93). B.M. (N.H.), Reg. Nos. 1963. 39-41.

	Ratios				Body Length (mm.)
	<i>a</i>	<i>b</i>	<i>c</i>	<i>V</i>	
Males	63.3	7.4	26.9		5.0
	65.4	7.5	28.2		5.3
	66.3	7.6	28.2		5.5
	65.5	7.3	27.9		5.7
Females	64.4	8.6	30.9	57.1	5.6
	63.7	9.4	31.7	58.6	5.8

MEASUREMENTS (in mm. in order of body lengths above). *Males*. Body breadth : 0.079 ; 0.081 ; 0.083 ; 0.087. Oesophagus length : 0.68 ; 0.71 ; 0.72 ; 0.78. Diameter of head : 0.028 ; 0.034 ; 0.032 ; 0.035. Length of cephalic setae, long/short : 0.026/0.014 ; 0.027/0.015 ; 0.027/0.016 ; 0.027/0.016. Length of paired cervical setae : 0.026 ; 0.025 ; 0.026 ; 0.026. Diameter of body at level of cervical setae : 0.048 ; 0.047 ; 0.048 ; 0.049. Length of pharyngeal rods : 0.097 ; 0.101 ; 0.098 ; 0.099. Distance of nerve ring from anterior end of body : 0.24 ; 0.23 ; 0.26 ; 0.26. Tail length : 0.186 ; 0.188 ; 0.195 ; 0.204. Cloacal diameter : 0.066 ; 0.067 ; 0.070 ; 0.069. Spicule length : 0.060 ; 0.058 ; 0.060 ; 0.060. Gubernaculum length : 0.030 ; 0.030 ; 0.028 ; 0.029.

Females. Body breadth : 0.087 ; 0.091. Oesophageal length : 0.65 ; 0.62. Diameter of head : 0.035 ; 0.036. Length of cephalic setae, long/short : 0.034/0.016 ; 0.034/0.014. Length of paired cervical setae : 0.027/0.029. Diameter of

body at level of cervical setae : 0.049 ; 0.046. Length of pharyngeal rods : 0.074 ; 0.076. Distance of nerve ring from anterior end of body : 0.27 ; 0.25. Tail length : 0.181 ; 0.183. Anal diameter : 0.059 ; 0.062. Distance of vulva from anterior end of body : 3.2 ; 3.4.

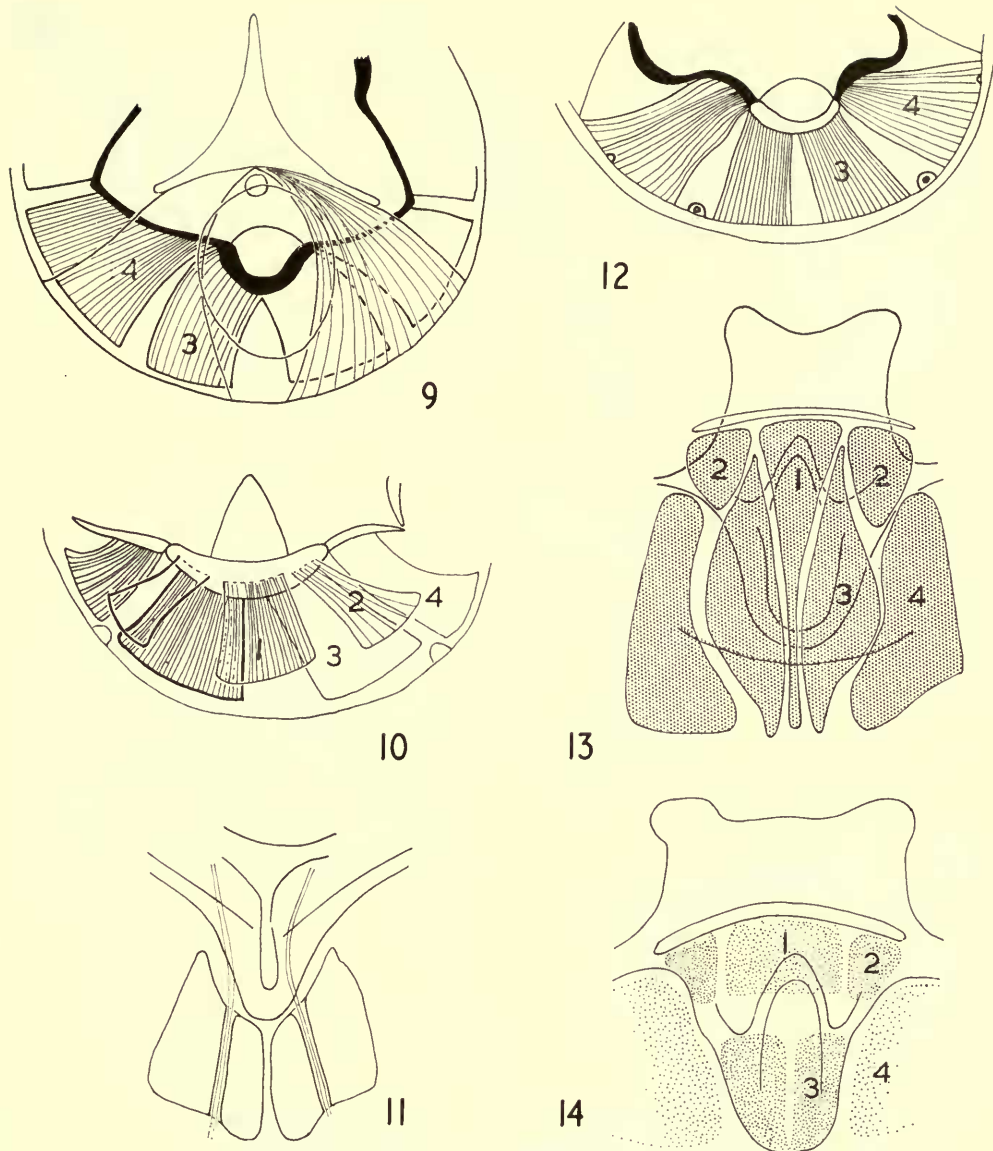
The head is similar in structure of that of *Trissonchulus janetae* Inglis, 1961 differing only in the presence of long cephalic setae (Text-figs. 189 and 192). There are two small paired solid cuticular onchia on the anterior end of the dorsal sector of the oesophagus and one large onchium on each ventro-lateral sector (Text-fig. 190). The cephalic setae lie in an outer circle and six are longer than the remaining four. The inner circle of labial sense organs is composed of six sessile papillae. There is a distinct cephalic capsule on the posterior edge of which lie the openings of the amphids which lead into large pockets (Text-fig. 189). Immediately posterior to each amphid is a doubled seta. This large structure appears at first to consist of two setae but the two components appear to be separate at the distal end only. In all the larvae there is a set of secondary teeth near the anterior end of the oesophagus (Text-fig. 193).

The tail is the same shape in both sexes (Text-fig. 194) and the caudal glands lie anterior to the cloacal or anal opening. In the male there is no pre-cloacal modification, the spicules are short and massive with bluntly capitate proximal and sharply pointed distal ends. The gubernaculum is small with a thin proximal end and stout distal end (Text-fig. 191). The testes are paired and opposed just as in *T. janetae*. Similarly the reproductive system of the female consists of two opposed uteri and associated reflexed ovaries, with very large eggs, 0.378×0.076 to 0.420×0.083 mm.

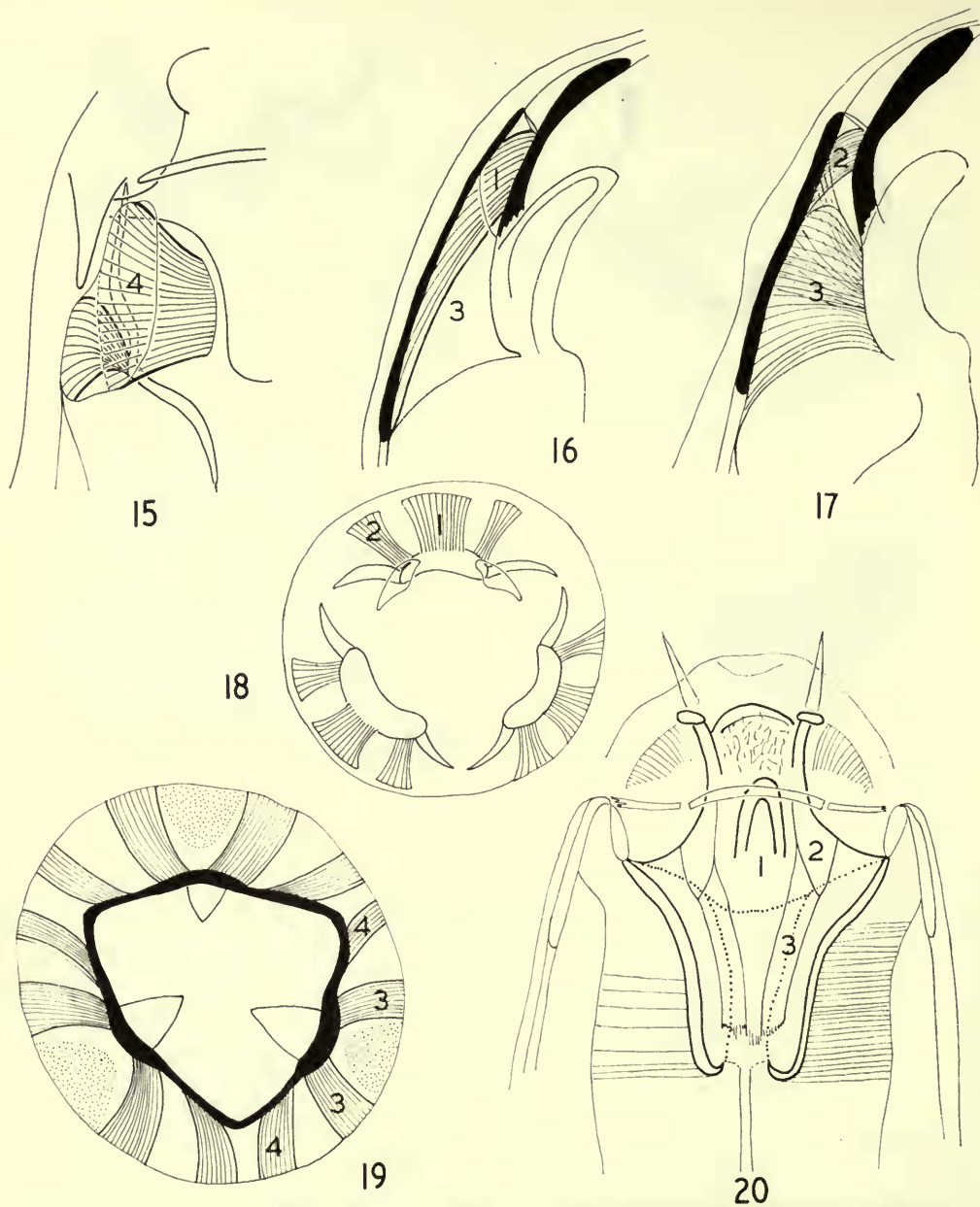
DISCUSSION

Currently the genus *Thalassironus* contains only two species, *T. britannicus* de Man, 1889 (recently redescribed from the types by Chitwood, 1960) and *T. bipartitus* (Wieser, 1953) (originally referred to *Parironus* Micoletzky, 1930 but transferred to *Thalassironus* by Chitwood (1960)). The present species differs from both these in the presence of the long "double" cervical setae, the great length of the cephalic setae and in the form of the spicules and gubernaculum.

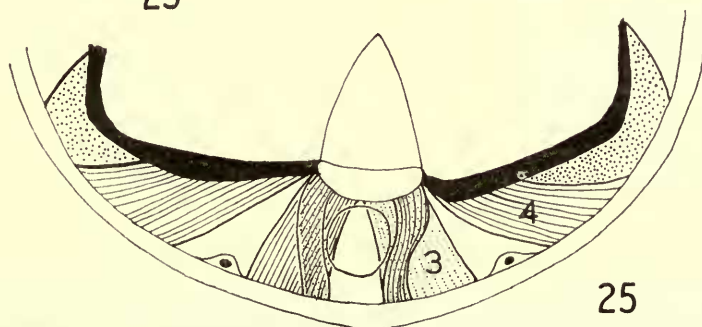
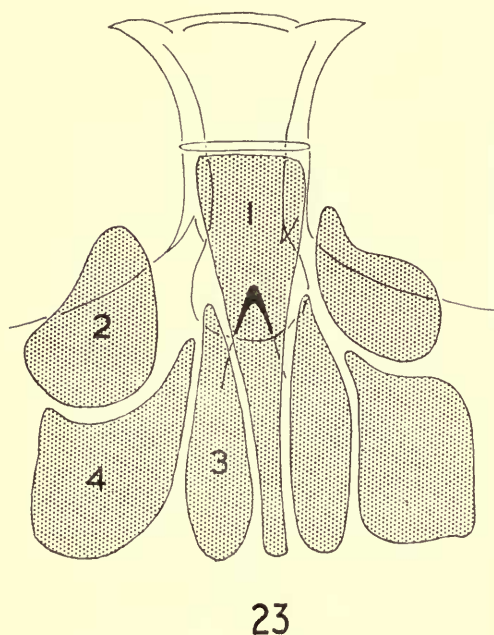
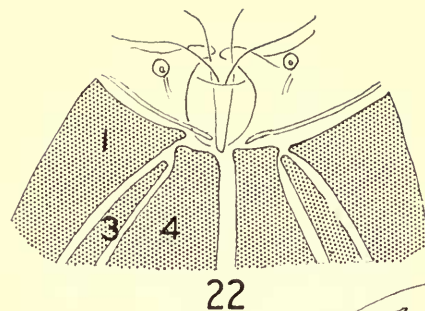
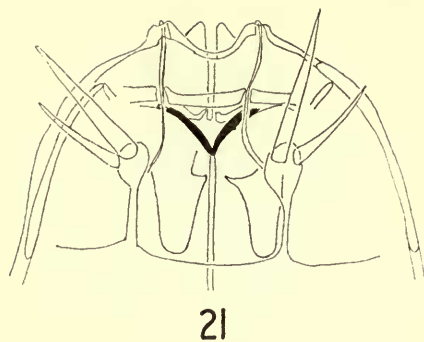
Text-figures 9-194
and References



FIGS. 9-14. *Mesonchium studiosa*. Fig. 9. Transverse section cut just posterior to onchium looking anteriorly showing general musculature of oesophagus, duct of oesophageal gland, the sudden expansion of the onchial cavity and the distribution of muscles-3 and -4. Fig. 10. *En face* view of distribution of oesophageal musculature. Fig. 11. View taken at end of a radius of the oesophagus showing distribution of origins of Muscles-4 and nerves to labial sense organs. Fig. 12. Transverse section just about mid-level of onchial plate. Fig. 13. Origins of oesophageal musculature. Fig. 14. Areas of insertion of musculature on onchial plate and flanking lining of oesophageal radii.

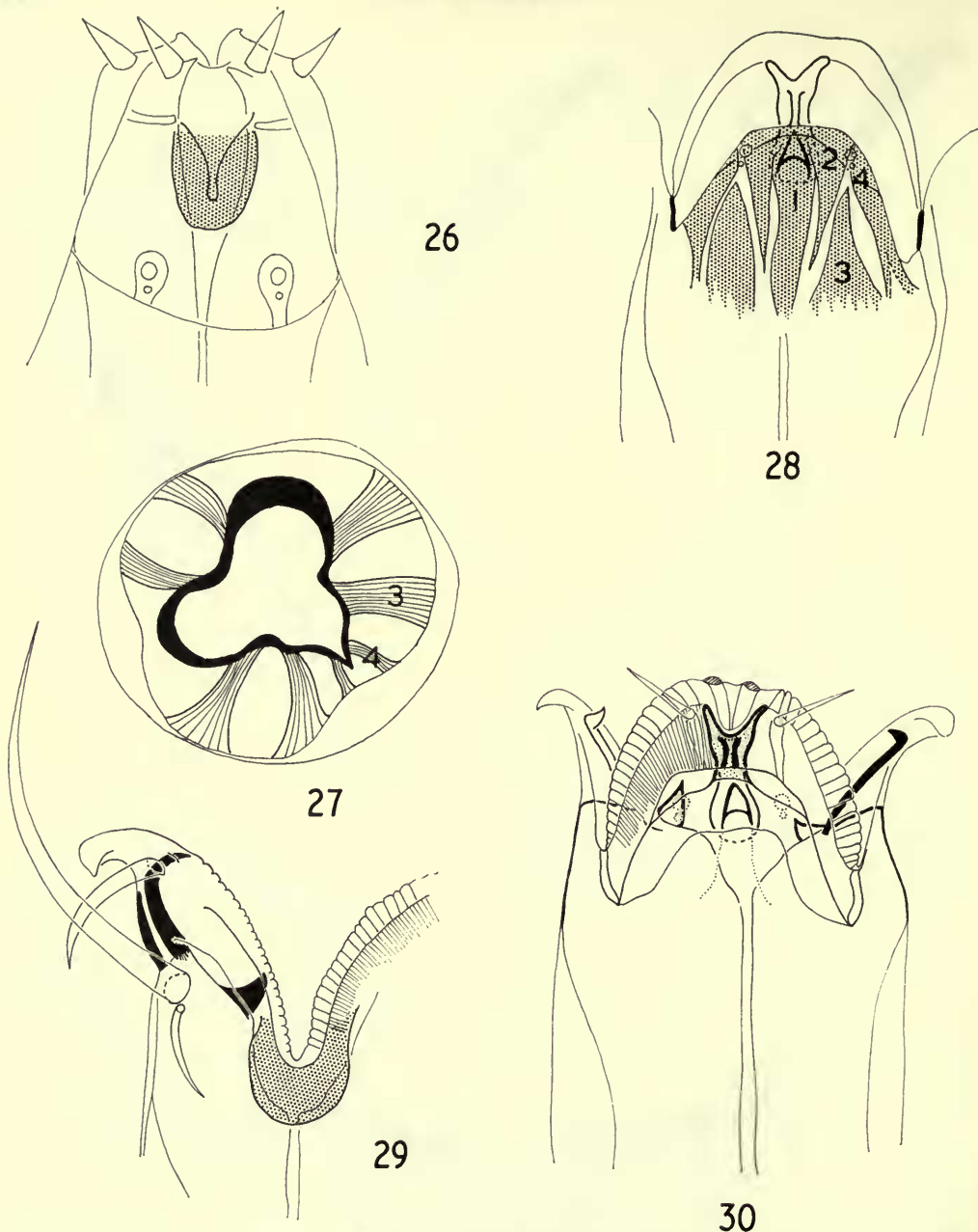


FIGS. 15-17. *Mesonchium studiosa*. Fig. 15. Distribution of Muscle-4. Fig. 16. Longitudinal section through head showing longitudinal distribution of Muscles-1 and -3. Fig. 17. The same showing distribution of Muscles-2 and -3. Note that the more lateral parts of Muscle-3 are directed posteriorly while the median part is fanned anteriorly. FIGS. 18-20. *Enoplolaimus mus*. Fig. 18. En face view of distribution of anterior ring of oesophageal muscles (compare with Fig. 10). Fig. 19. Transverse section about level of origin of onchium. Fig. 20. Origins of oesophageal musculature.



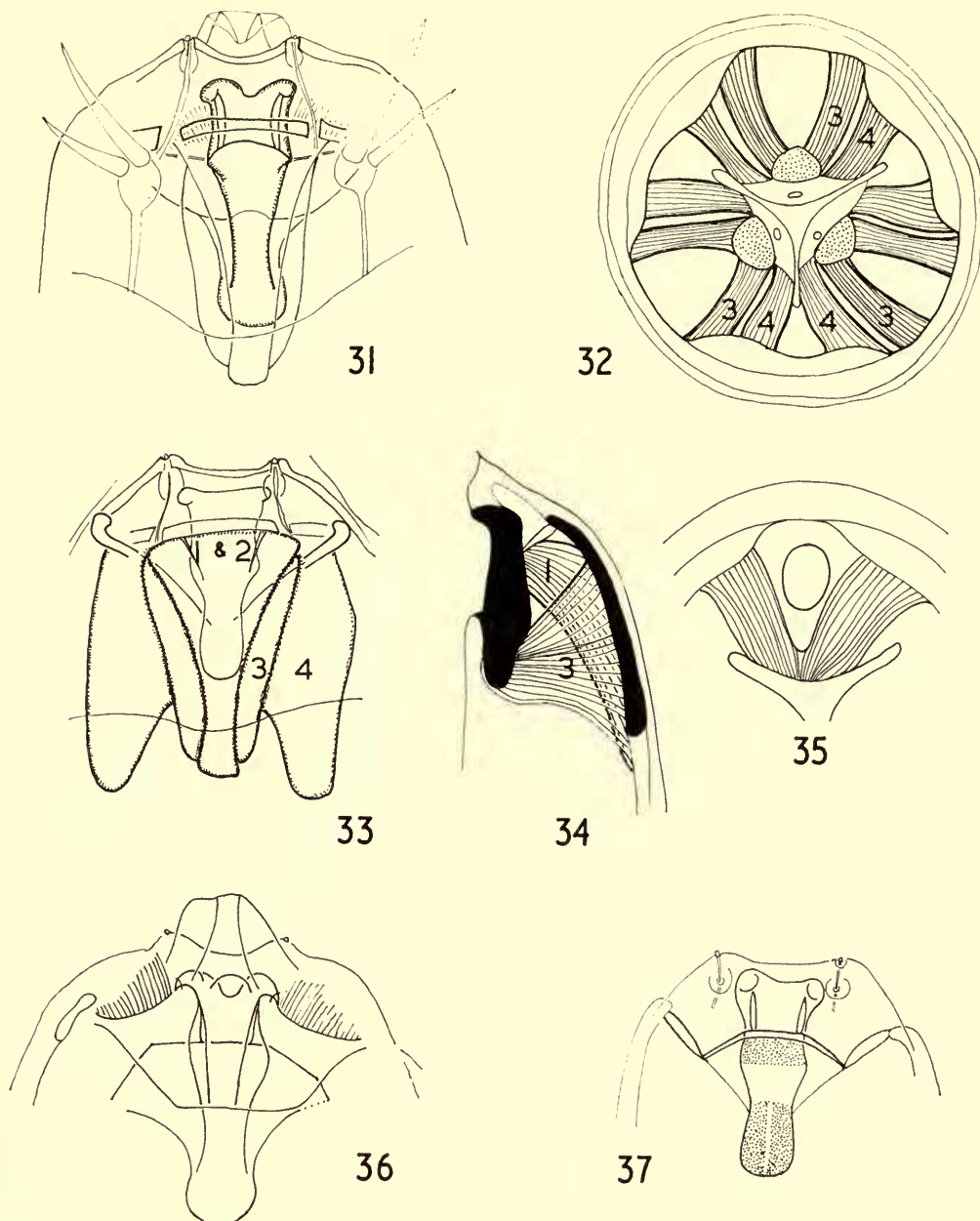
FIGS. 21 and 22. *Enoplus harlockae*. Fig. 21. View taken at end of a radius of oesophagus showing distribution of nerves to labial sense organs and the position of the radial process (solid black) relative to the cephalic ring. Fig. 22. Distribution of muscle origins at a radius.

FIGS. 23-25. *Africanthion nudus*. Fig. 23. Origins of oesophageal musculature. Fig. 24. Longitudinal section through one lip showing distribution of Muscle-1. Fig. 25. Transverse section just posterior to onchium showing very narrow general oesophageal musculature enfolding oesophageal gland duct, the distribution of Muscles-3 and -4 and the massive radial process (solid black).

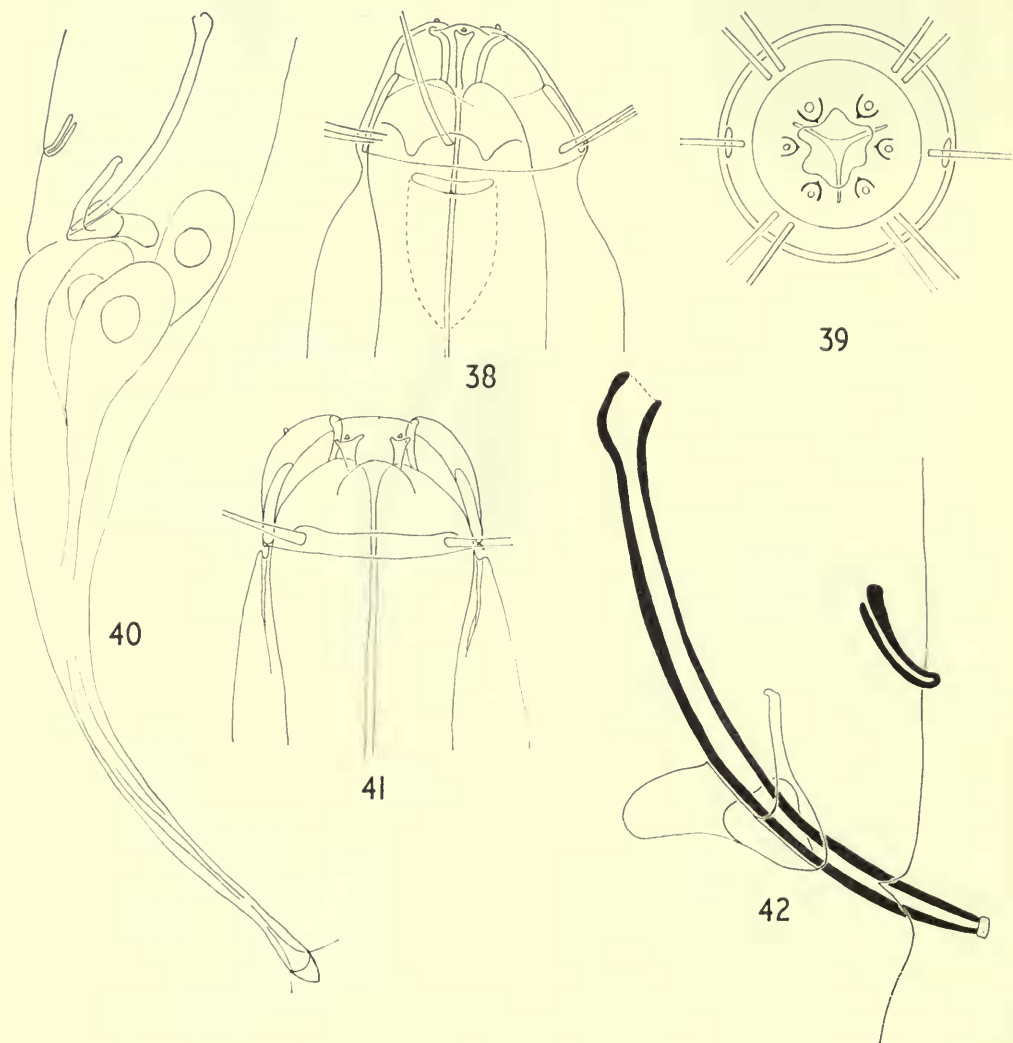


FIGS. 26 and 27. *Trileptium ayum*. Fig. 26. View taken at the end of a radius showing extensive radial mass (stippled) and the extreme posterior level at which the radial processes articulate relative to the cephalic ring. Fig. 27. Obliquely transverse section showing relatively small Muscles-4 and the way in which they disappear (upper left side of figure) before full development of onchium. (The section is cut more posteriorly on the lower right side of the figure.)

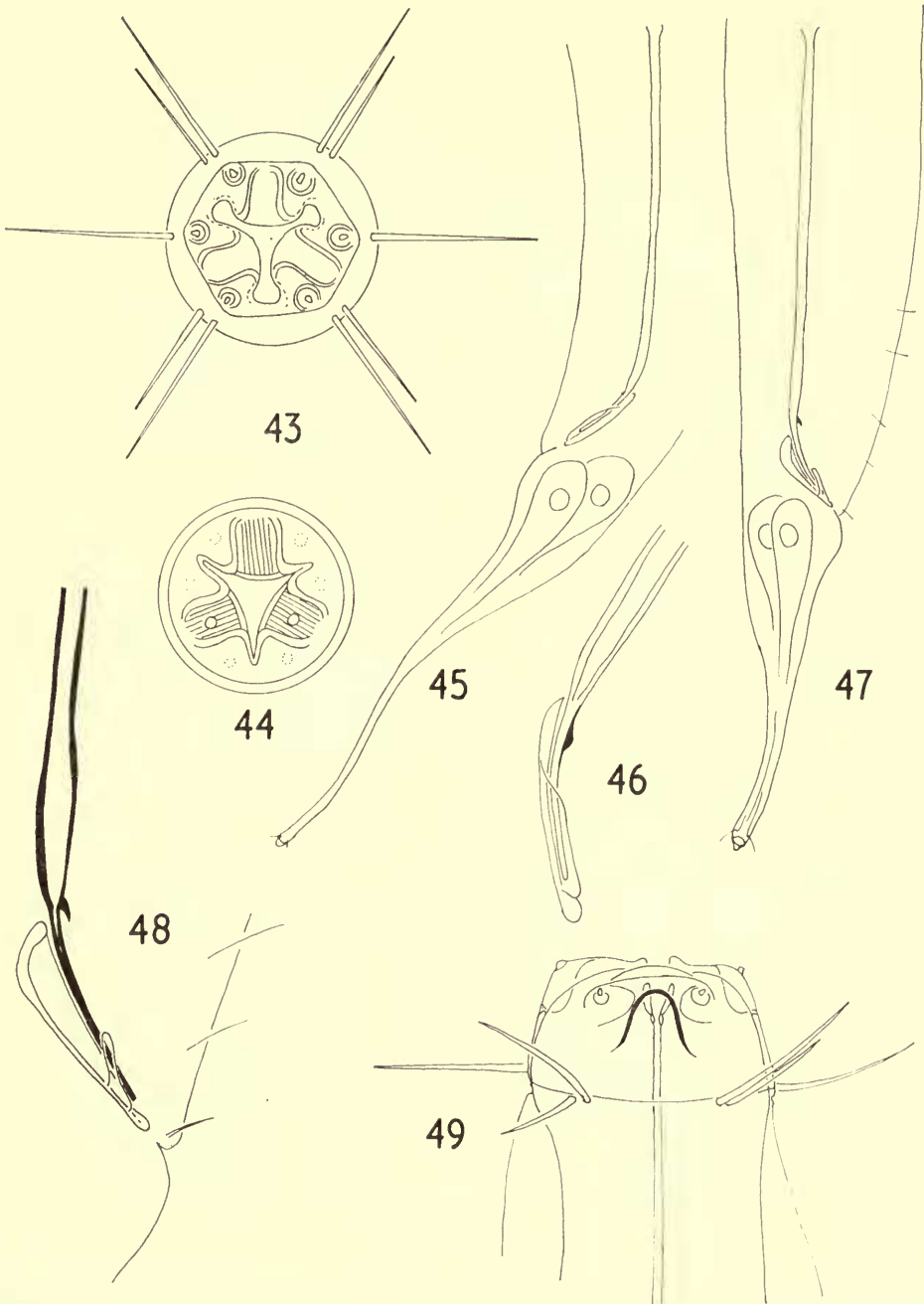
FIGS. 28-30. *Enoploides* sp. Fig. 28. Origins of oesophageal musculature. Note partial fusion of Muscles-1 and -2. Fig. 29. View taken at the end of one radius showing radial mass (stippled), striated outer rim to lips, light mandibles and supplementary strengthening structure in outer cuticle at same level as mandible. Fig. 30. Dorsal view of head.



FIGS. 31-37. *Enoplus harlockae*. Fig. 31. Dorsal view of lip showing form of mandibular : onchial-plate complex. Fig. 32. Transverse section at level of posterior third of complex. Note attachment of oesophagus to body wall. Fig. 33. Origins of oesophageal musculature. Fig. 34. Longitudinal section showing distribution of Muscles-1 and -3. Fig. 35. Transverse section posterior to onchial complex showing distribution of general oesophageal musculature relative to duct of oesophageal gland. Fig. 36. Inner view of lip. Fig. 37. Exterior view of lip under pressure showing insertions of oesophageal musculature (stippled) and the form of the onchial plate, the mandibular ring and the radial masses.

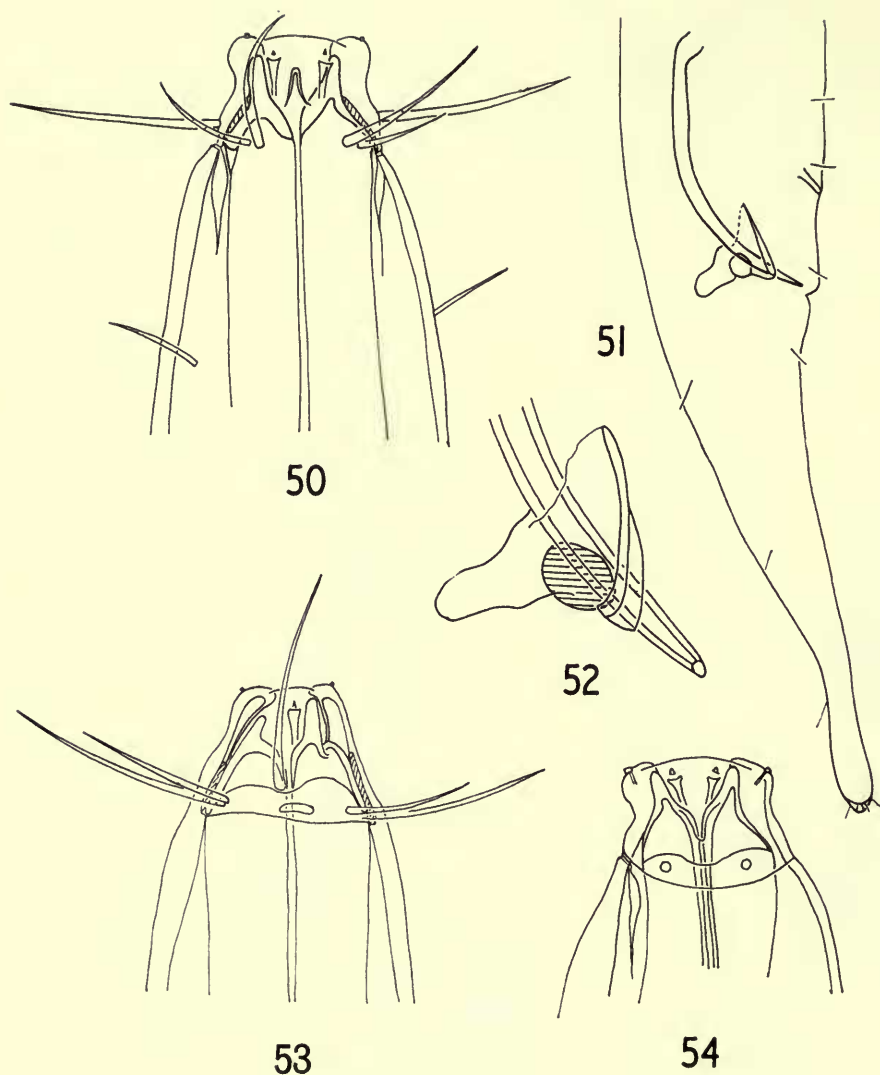


FIGS. 38-42. *Dayellus dayi*. Fig. 38. Lateral view of head with dorsal surface to the left. Fig. 39. *En face* view of head. Fig. 40. Lateral view of male tail. Fig. 41. Dorsal view of head. Fig. 42. Detail of spicules and gubernaculum from the lateral aspect. Note particularly the square capped posterior end to the spicule.

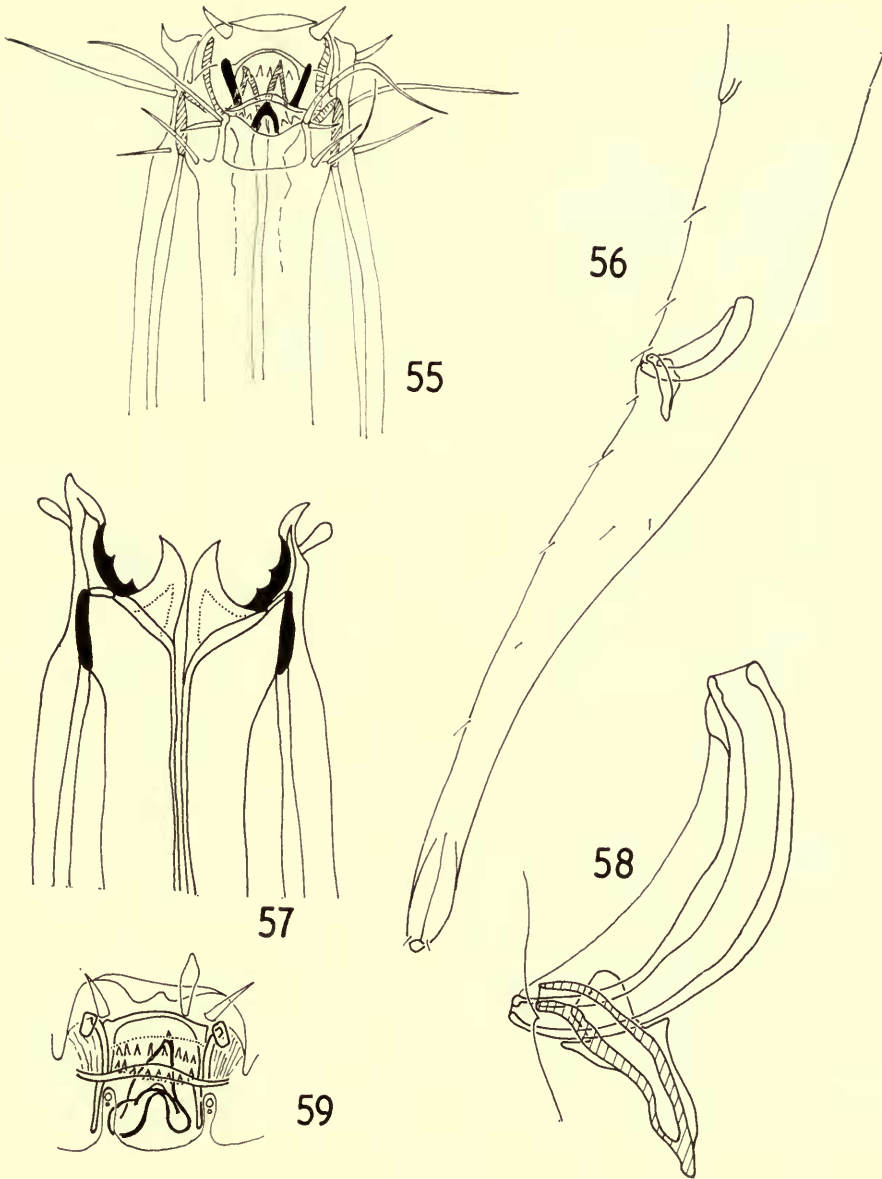


FIGS. 43, 44, 47-49. *Crenopharynx eina*. Fig. 43. En face view of head. Fig. 44. Deep en face optical section of head about level at which the three anterior prolongations of the oesophageal sectors separate. The solid circles are the ducts of the ventro-lateral oesophageal glands while the dotted circles represent the nerves which supply the labial sense organs. Fig. 47. Lateral view of male tail. Fig. 48. Detail of posterior end of spicules, showing large barb, and form of the gubernaculum. Fig. 49. Dorsal view of head.

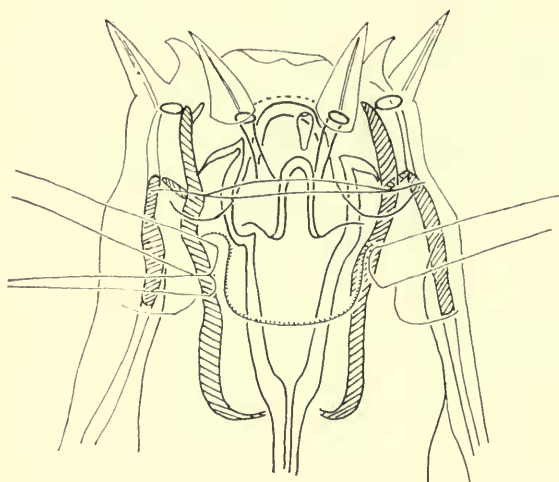
FIGS. 45-46. *Crenopharynx afra*. Fig. 45. Lateral view of male tail. Fig. 46. Detail



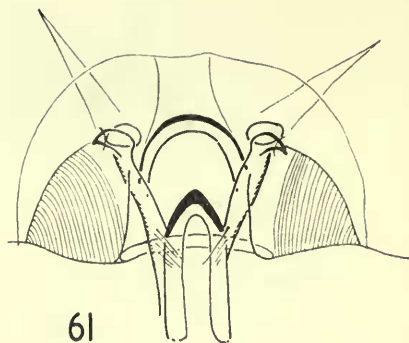
FIGS. 50-54. *Phanoderma unica*. Fig. 50. Dorsal view of head. Fig. 51. Lateral view of male tail. Fig. 52. Detail of gubernaculum. Fig. 53. Lateral view of head with dorsal surface to the left. Fig. 54. Ventral view of head. Cephalic setae not drawn for clarity.



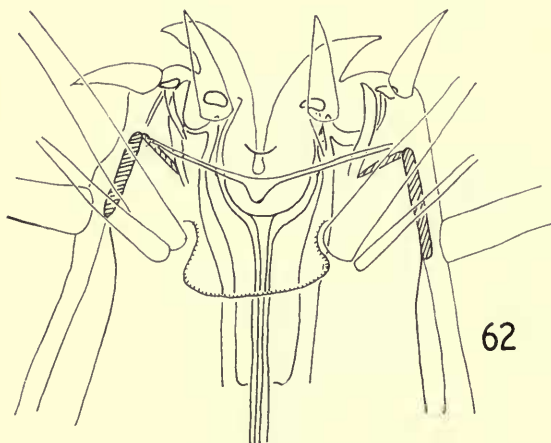
FIGS. 55-59. *Oxyonchus dittevseni*. Fig. 55. Dorsal view of head. Fig. 56. Male tail from the lateral aspect. Fig. 57. Optical section through head, from dorsal surface, at level of cephalic cirri. Fig. 58. Detail of gubernaculum and spicules. Fig. 59. Detail of ventro-lateral lip, with dorsal surface to the right, showing distinct mandibular rods, cephalic cirrus and distribution of small denticles on inner surface of mandibular plate.



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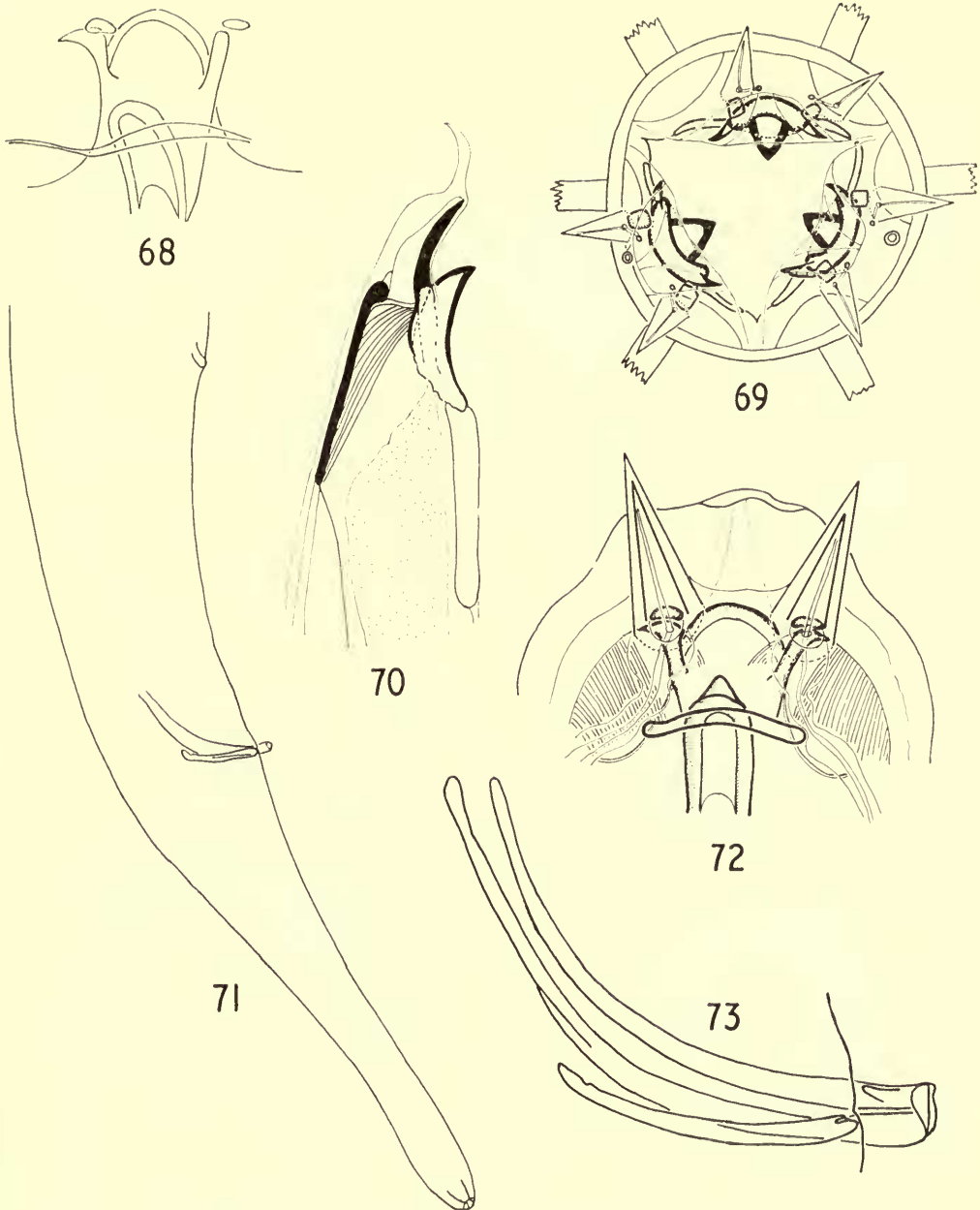


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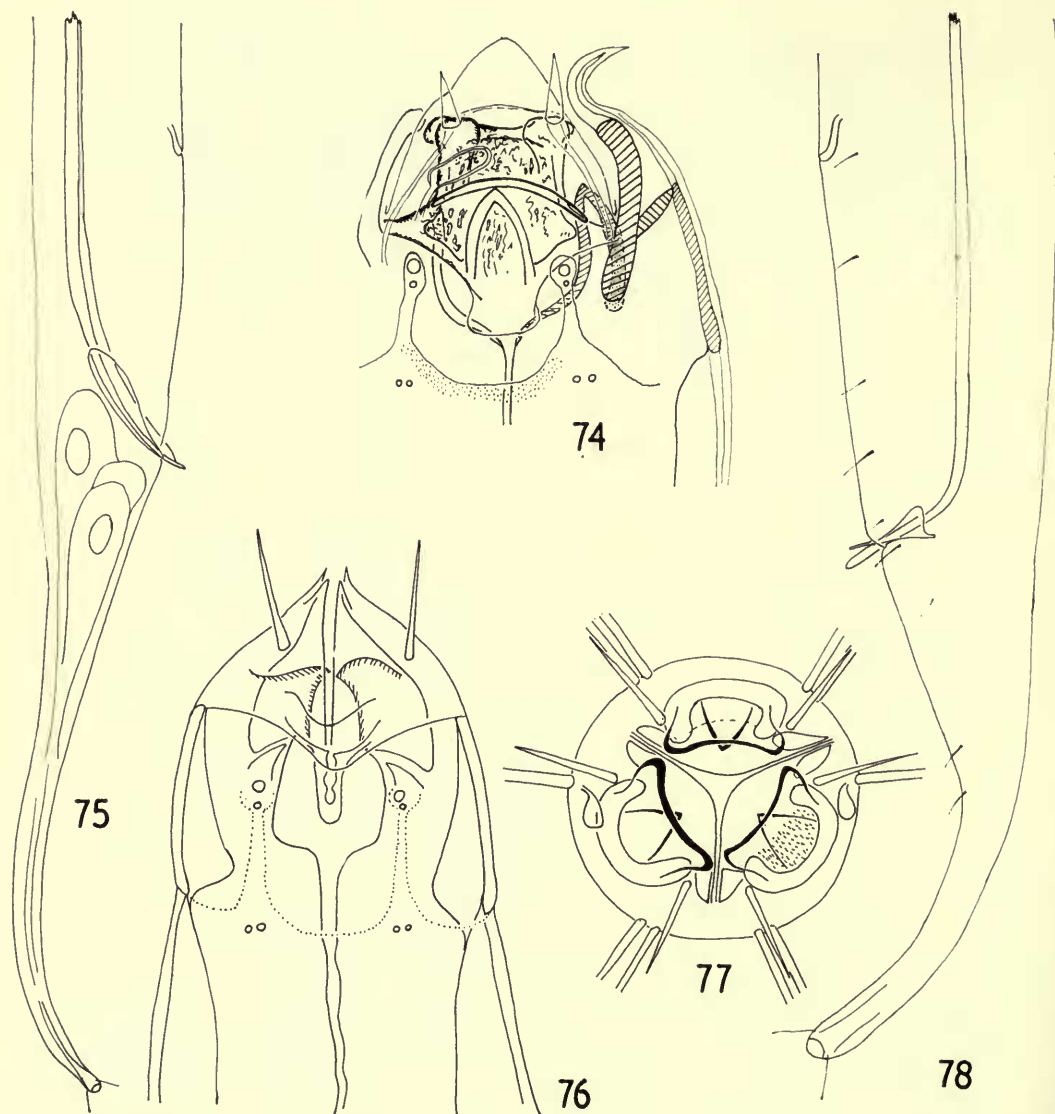


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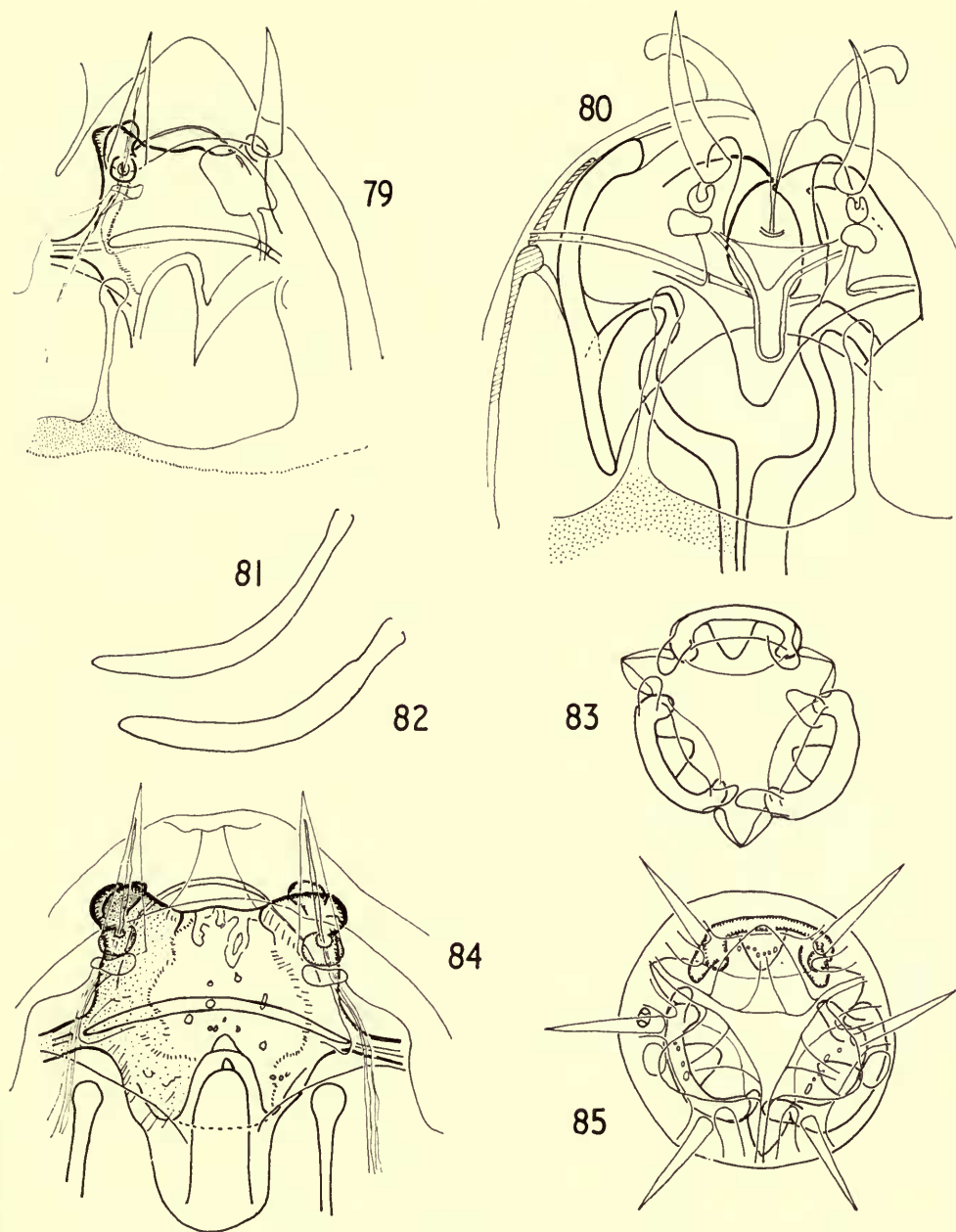
FIGS. 60-67. *Enoplolaimus mus* Fig. 60. Ventro-lateral view of head showing cephalic capsule and mandibular : onchial complex in optical section (cross-hatched). Fig. 61. View of lip from inner surface. Fig. 62. Ventral view of head. Figs. 63-66. Optical *en face* sections of mandibular : onchial-plate complex, from posterior end (63) anteriorly (66). Note separation of mandibular rods from mandibular plate at levels indicated in Figs. 64 and 65. Fig. 67. Composite *en face* view of complex.



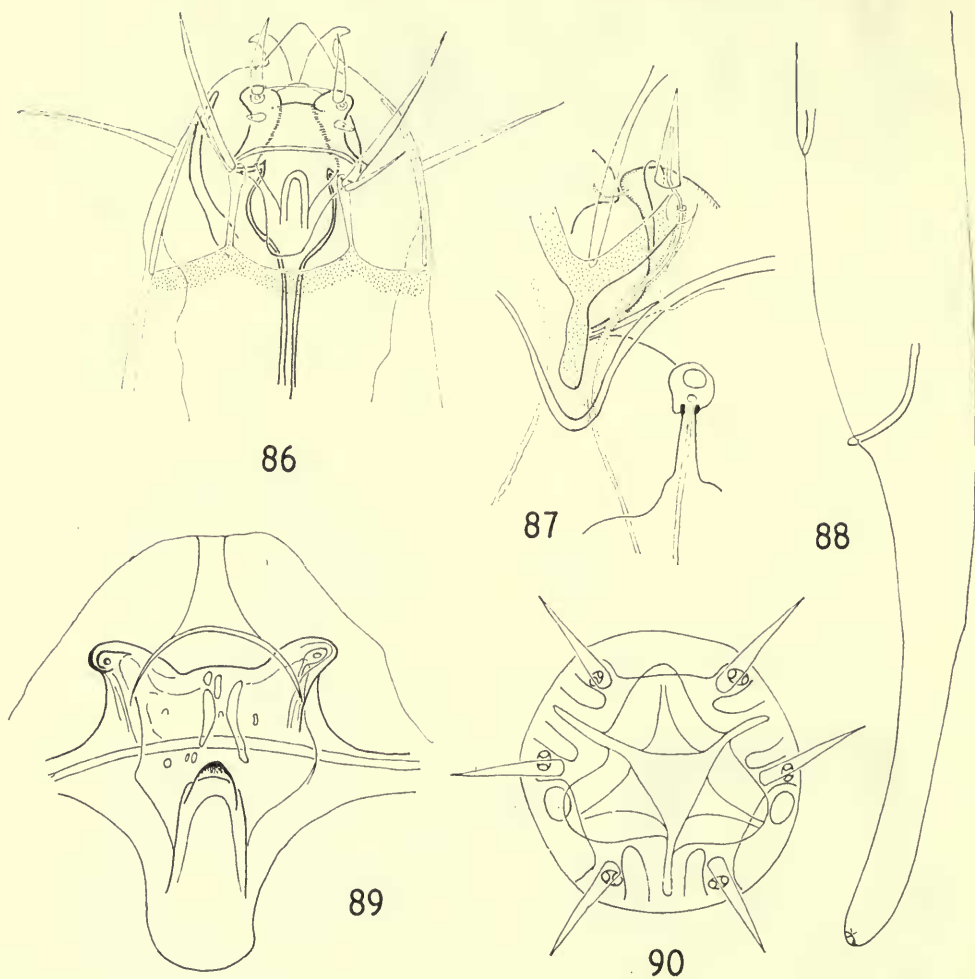
FIGS. 68-73. *Enoplolaimus mus*. Fig. 68. Mandibular : onchial complex, slightly from side, showing separation of mandibular rods and mandibular plate. Fig. 69. *En face* view of head with lip-lobes folded posteriorly over lips. Fig. 70. Longitudinal section of lip showing distribution of Muscle-1 and posterior extension of onchial cavity (pocketed condition : see page 279). Fig. 71. Lateral view of male tail. Fig. 72. Dorsal lip from outer surface showing distribution of nerves to labial sense organs relative to cephalic ring and mandibular complex. Fig. 73. Detail of spicules and gubernaculum. Note the barbed posterior end to spicule.



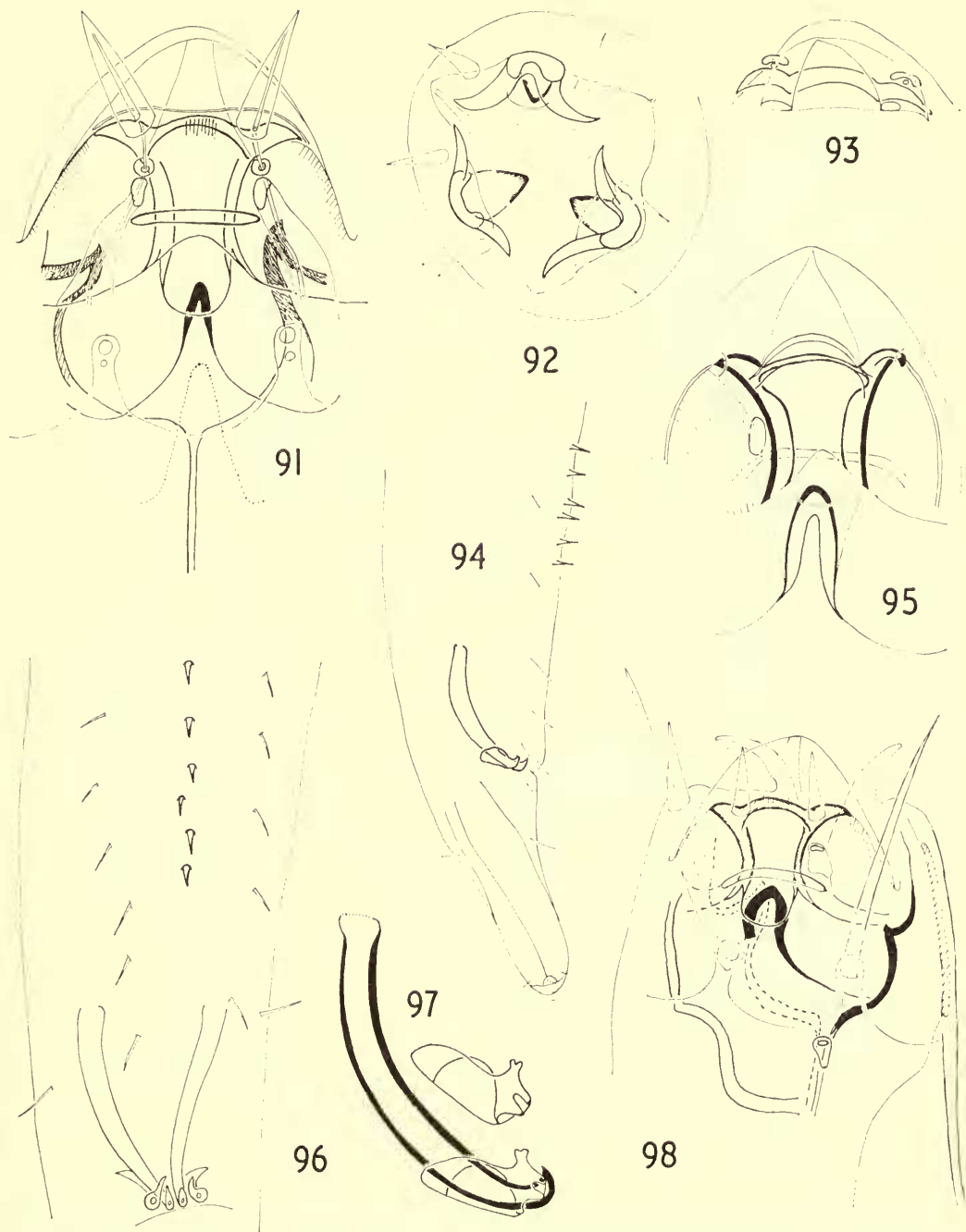
FIGS. 74 and 75. *Mescanthion ceeus*. Fig. 74. Dorsal lip from outer surface. Fig. 75. Lateral view of male tail (spicule not shown completely because of its length).
 FIGS. 76-78. *M. cavei*. Ventral view of head. Fig. 77. Simplified *en face* view of head.
 Fig. 78. Lateral view of male tail (spicule not shown completely).



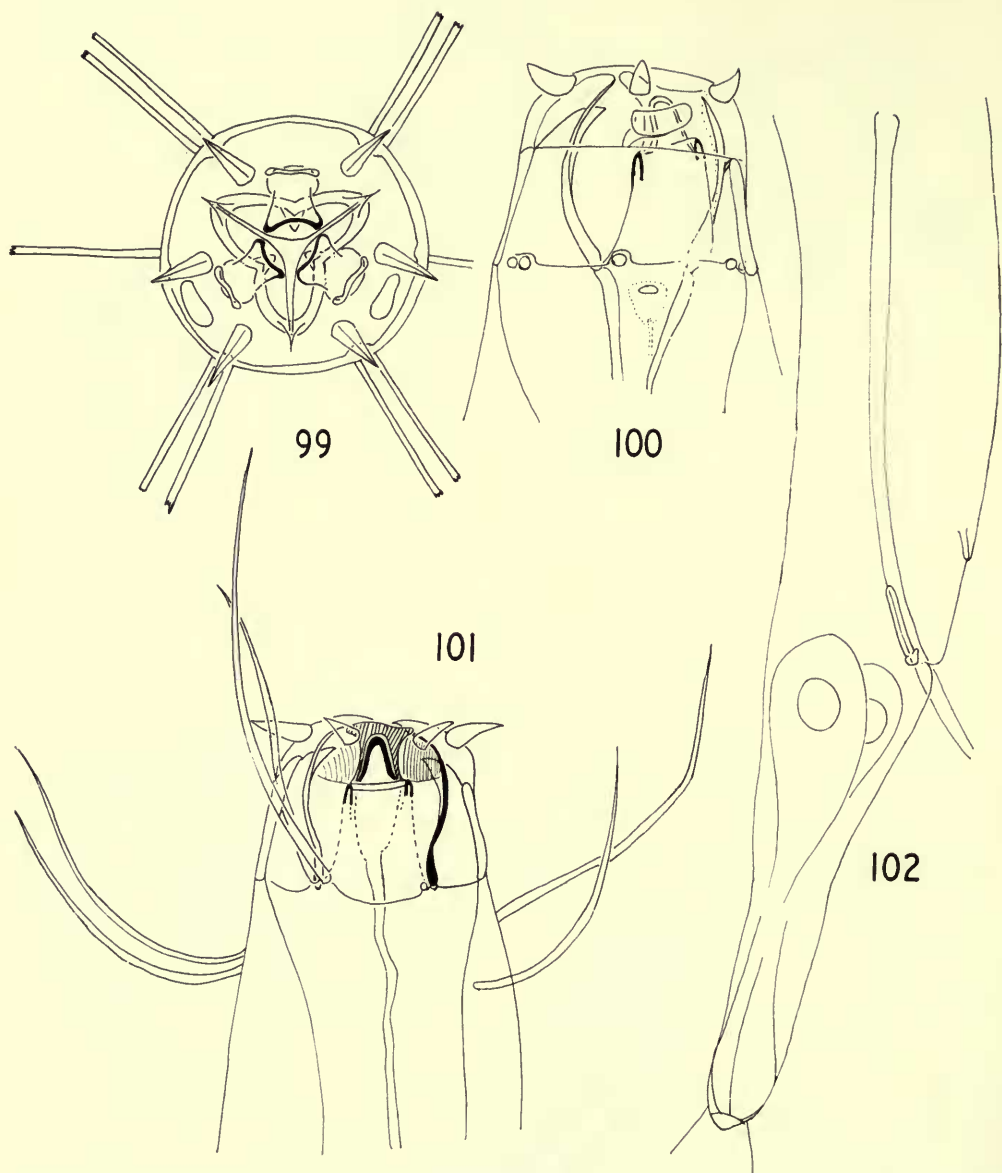
FIGS. 79-85. *Mesacanthion studiosa*. Fig. 79. Left ventro-lateral lip from the outer surface showing large pocket of cephalic slit and distribution of nerve to labial sense organ. Fig. 80. Ventral view of head showing cephalic capsule and mandibular : onchial complex in optical section. Figs. 81 and 82. Representative spicules. Fig. 83. *En face* view of mandibular : onchial complex. Fig. 84. Detail of dorsal lip from outer surface showing distribution of nerves to labial sense organs, cephalic ring, almost wholly absorbed mandibular rods and massive fusion of mandibular and onchial components of skeletal system. Fig. 85. *En face* view of head.



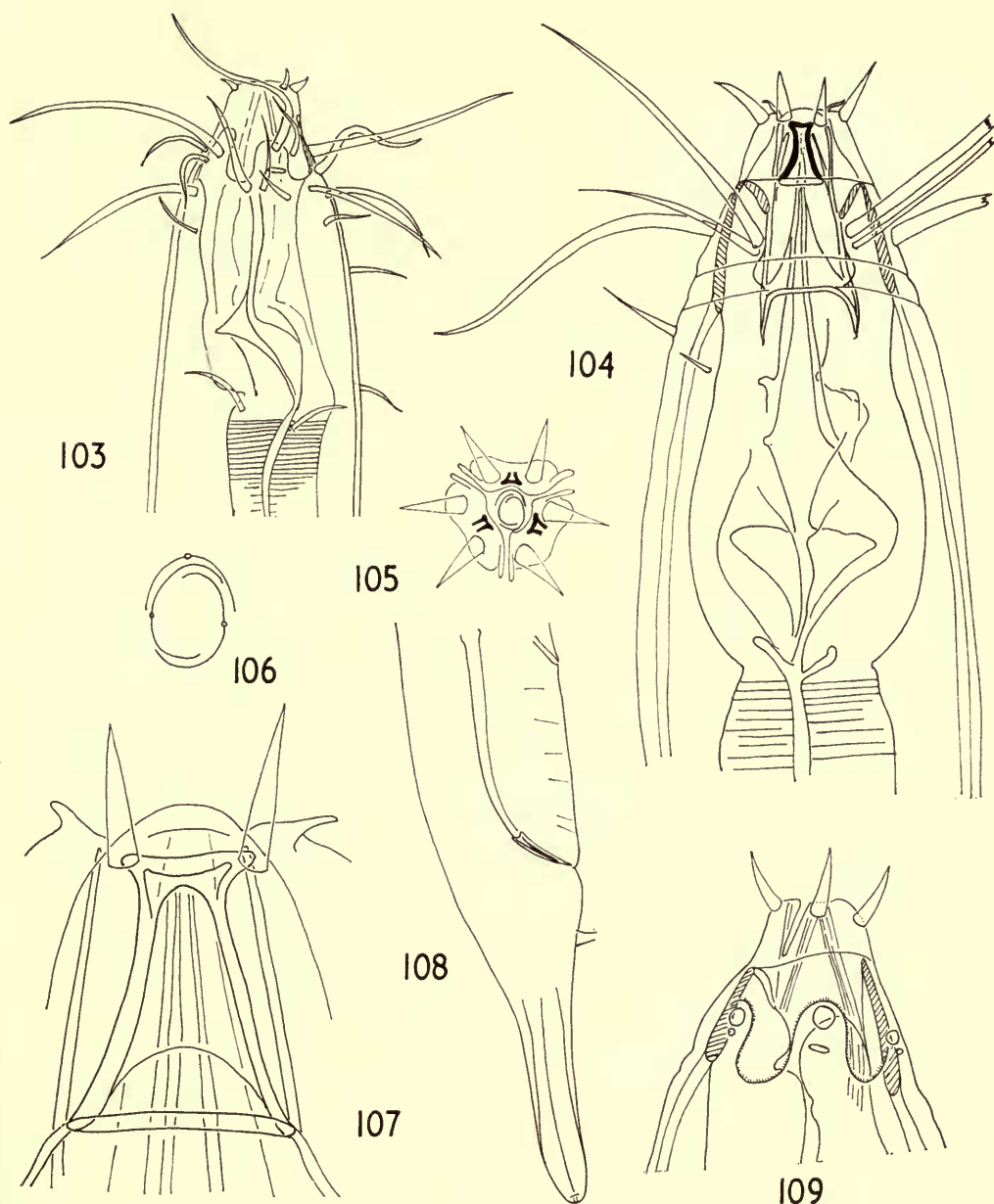
FIGS. 86-90. *Mescanthion studiosa*. Fig. 86. General dorsal view of head. Fig. 87. View taken at end of a radius showing distribution of nerve to labial sense organ and its relationship to cephalic ring. Fig. 88. Lateral view of male tail. Fig. 89. View of lip from inner surface. Fig. 90. *En face* view of head showing anterior modifications of cephalic capsule.



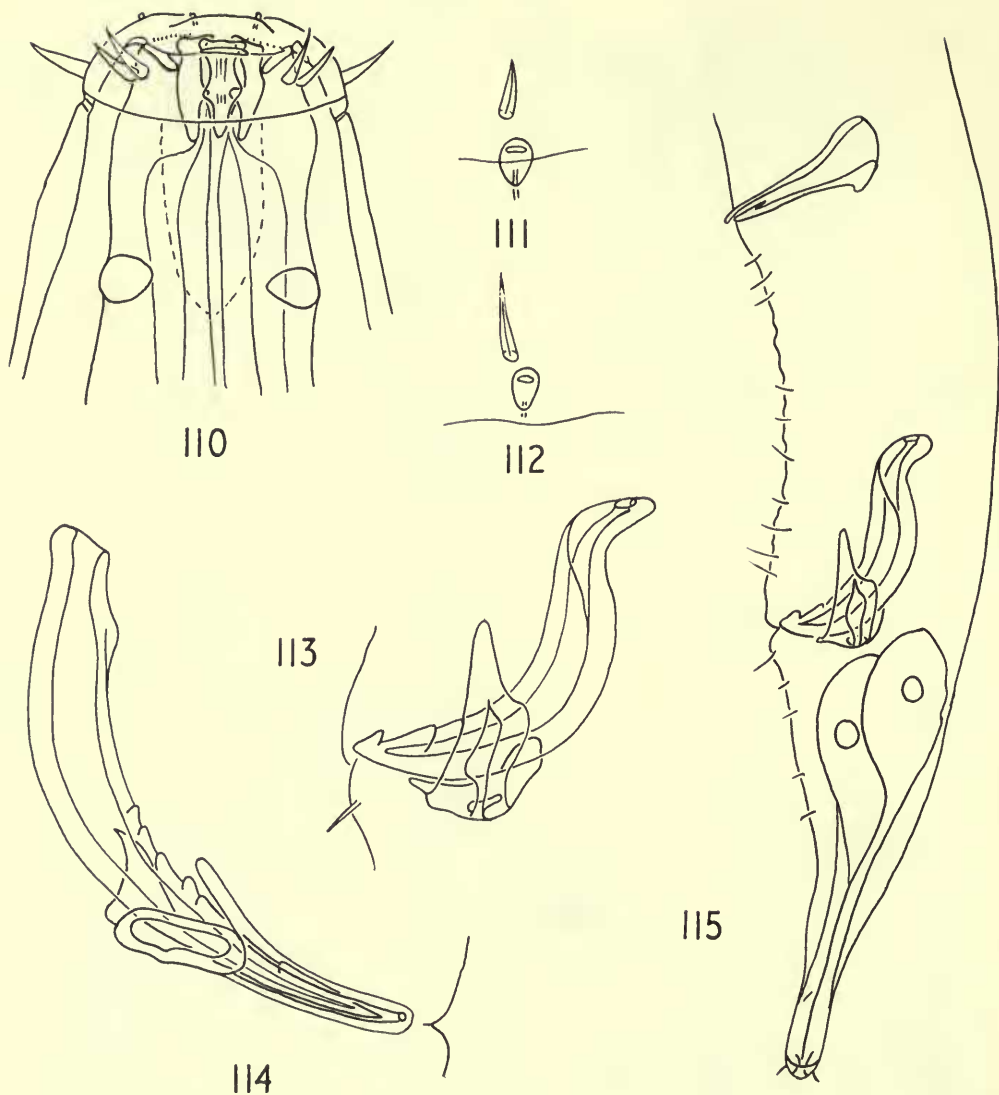
FIGS. 91-98. *Africanthion nudus*. Fig. 91. Dorsal lip from outer surface. Fig. 92. En face view of head. Fig. 93. En face detail of mandible showing thickenings of edges of labial lobes. Fig. 94. Lateral view of male tail. Fig. 95. Left ventro-lateral lip from the inner surface. Fig. 96. Ventral view of male body anterior to cloacal opening showing distribution of pre-cloacal setae. Fig. 97. Detail of spicules and gubernaculum from the lateral aspect. Fig. 98. Left ventro-lateral lip from the outer surface showing small amphid and cephalic slit.



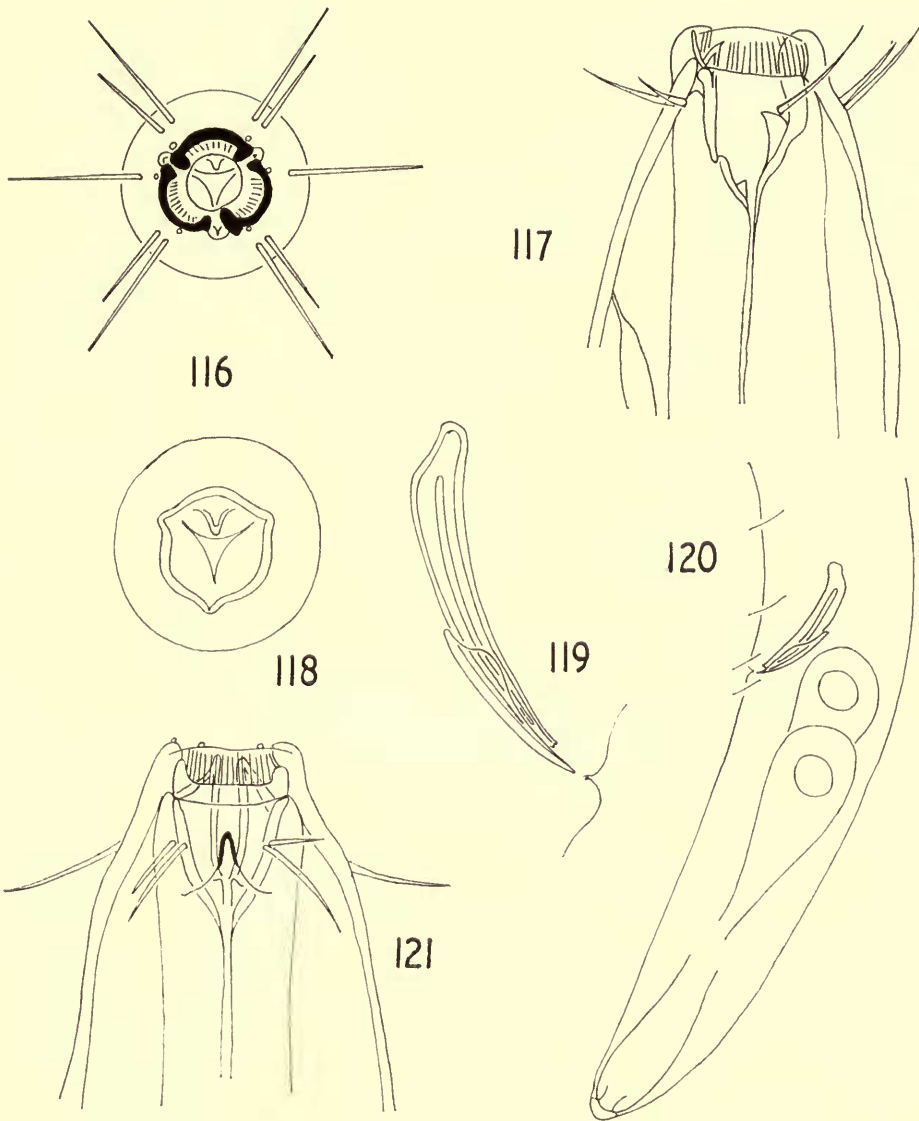
FIGS. 99-102. *Trileptium ayum*. Fig. 99. *En face* view of head. Fig. 100. Lateral view of head with the dorsal surface to the left. Fig. 101. Dorsal view of head. Note particularly the way in which the onchium is closely embraced by the mandible. Fig. 102. Lateral view of male tail.



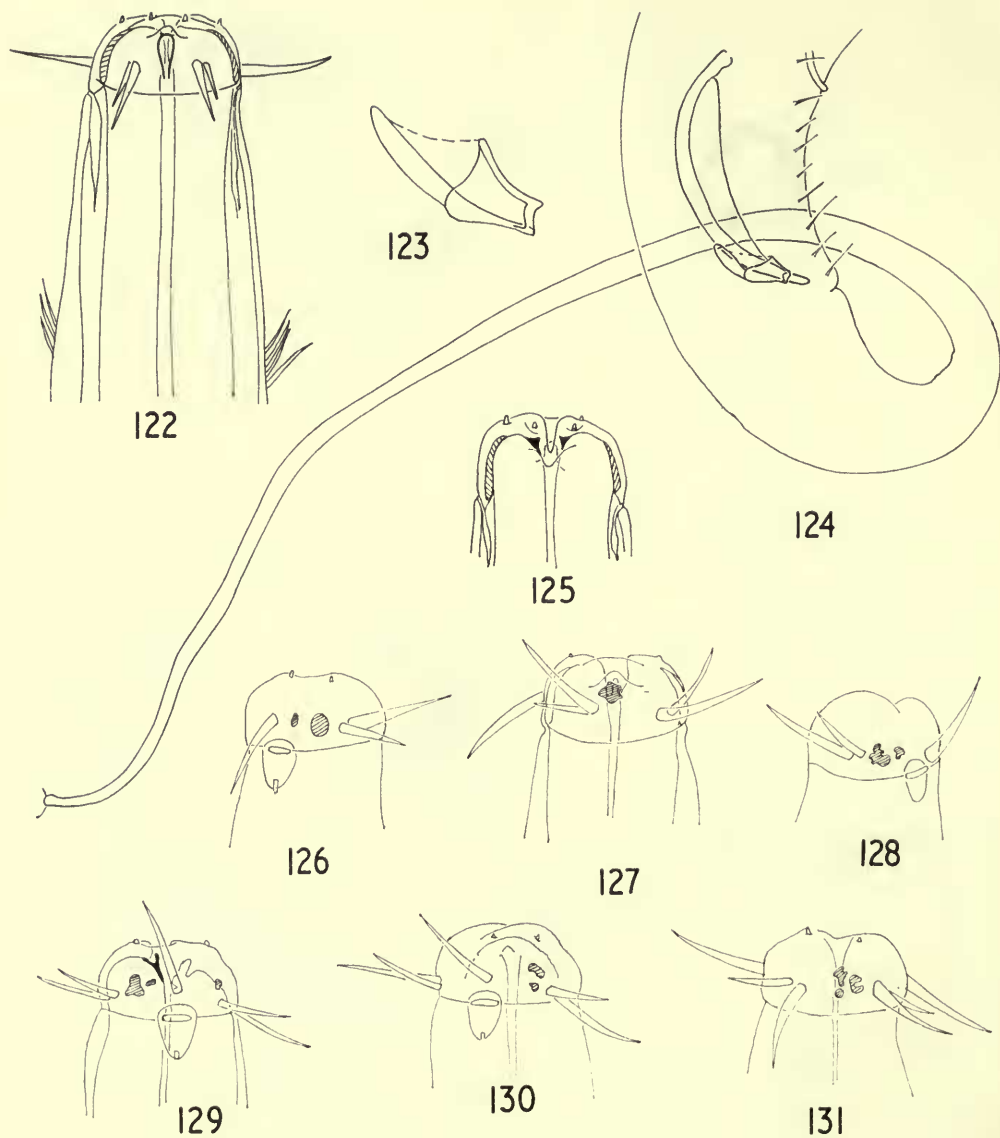
FIGS. 103-109. *Thoracostomopsis carolae*. Fig. 103. General view of male head from the lateral aspect. Fig. 104. Dorsal view of female head. Fig. 105. *En face* view of head. Fig. 106. Diagram of *en face* appearance of plate-like onchia. Fig. 107. Free-hand sketch of anterior, mandibular, part of dorsal lip. Fig. 108. Lateral view of male tail. Fig. 109. Detail of cephalic capsule from the lateral aspect.



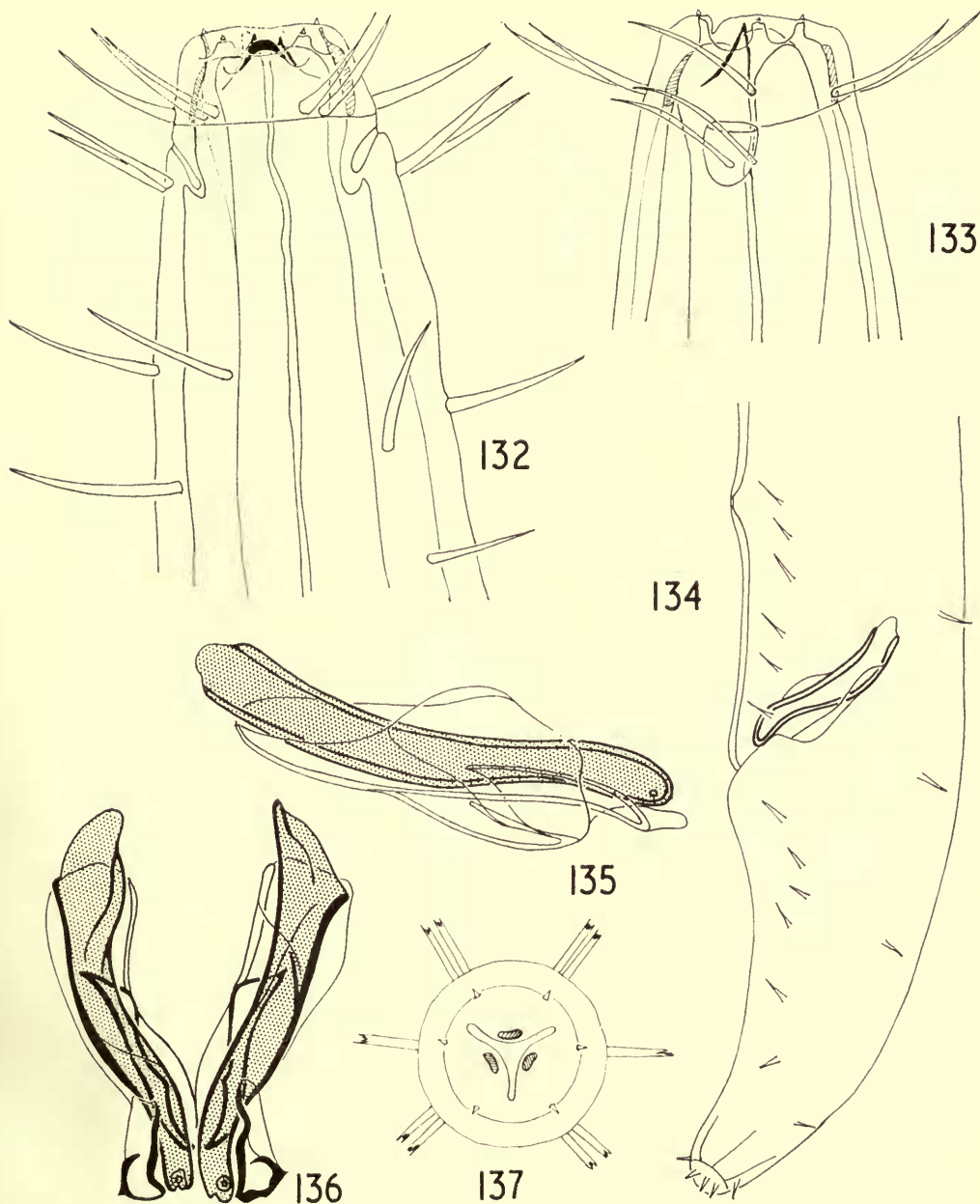
FIGS. 110-115. *Enoplus*. Fig. 110. *E. harlockae*. Dorsal view of head. Fig. 111. *E. harlockae*. Relationship of amphid to posterior edge of cephalic capsule. Fig. 112. *E. michaelsoni*. Relationship of amphid to posterior edge of cephalic capsule. Fig. 113. *E. harlockae*. Detail of spicules and gubernaculum. Fig. 114. *E. michaelsoni*. Detail of spicules and gubernaculum. Fig. 115. *E. harlockae*. Lateral view of male tail.



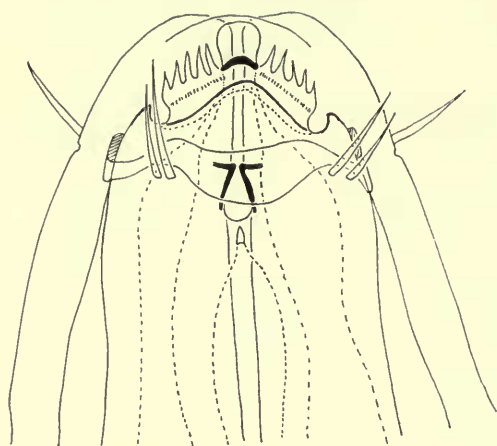
FIGS. 116-121. *Rhabdodemia nancyae*. Fig. 116. *En face* view of head. Fig. 117. Lateral view of head with the dorsal surface to the right. Fig. 118. *En face* optical section through onchial cavity showing large dorsal onchium. Fig. 119. Detail of spicules and gubernaculum. Fig. 120. Lateral view of male tail. Fig. 121. Dorsal view of head.



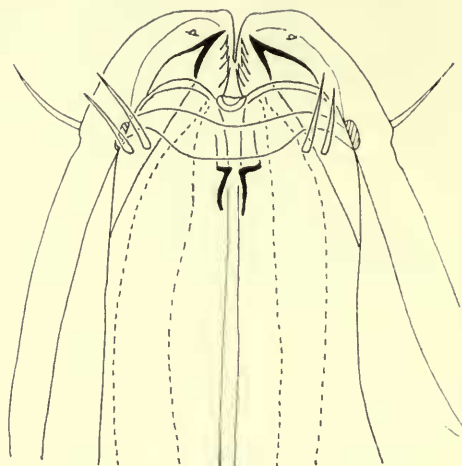
FIGS. 122-131. *Anticoma chitwoodi*. Fig. 122. Dorsal view of head. Fig. 123. Detail of gubernaculum. Fig. 124. Lateral view of male tail. Fig. 125. Ventral view of head. Figs. 126-131. Views of head showing lacunae in cephalic capsule. Fig. 126, left dorso-lateral; Fig. 127, dorsal; Fig. 128, right dorso-lateral; Fig. 129, left lateral; Fig. 130, right ventro-lateral; Fig. 131, ventral.



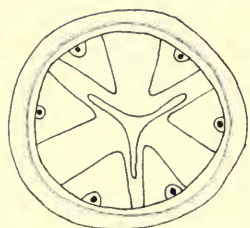
FIGS. 132-137. *Parabarbonema barba*. Fig. 132. Dorsal view of anterior end of body. Fig. 133. Lateral view of head with the dorsal surface to the left. Fig. 134. Lateral view of male tail. Fig. 135. Detail of spicules and gubernaculum from the lateral aspect. The spicule is stippled. Fig. 136. Ventral view of spicules and gubernaculum. The spicules are stippled. Fig. 137. *En face* view of head.



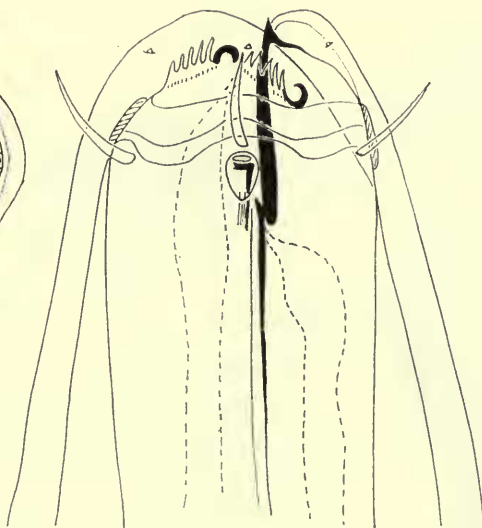
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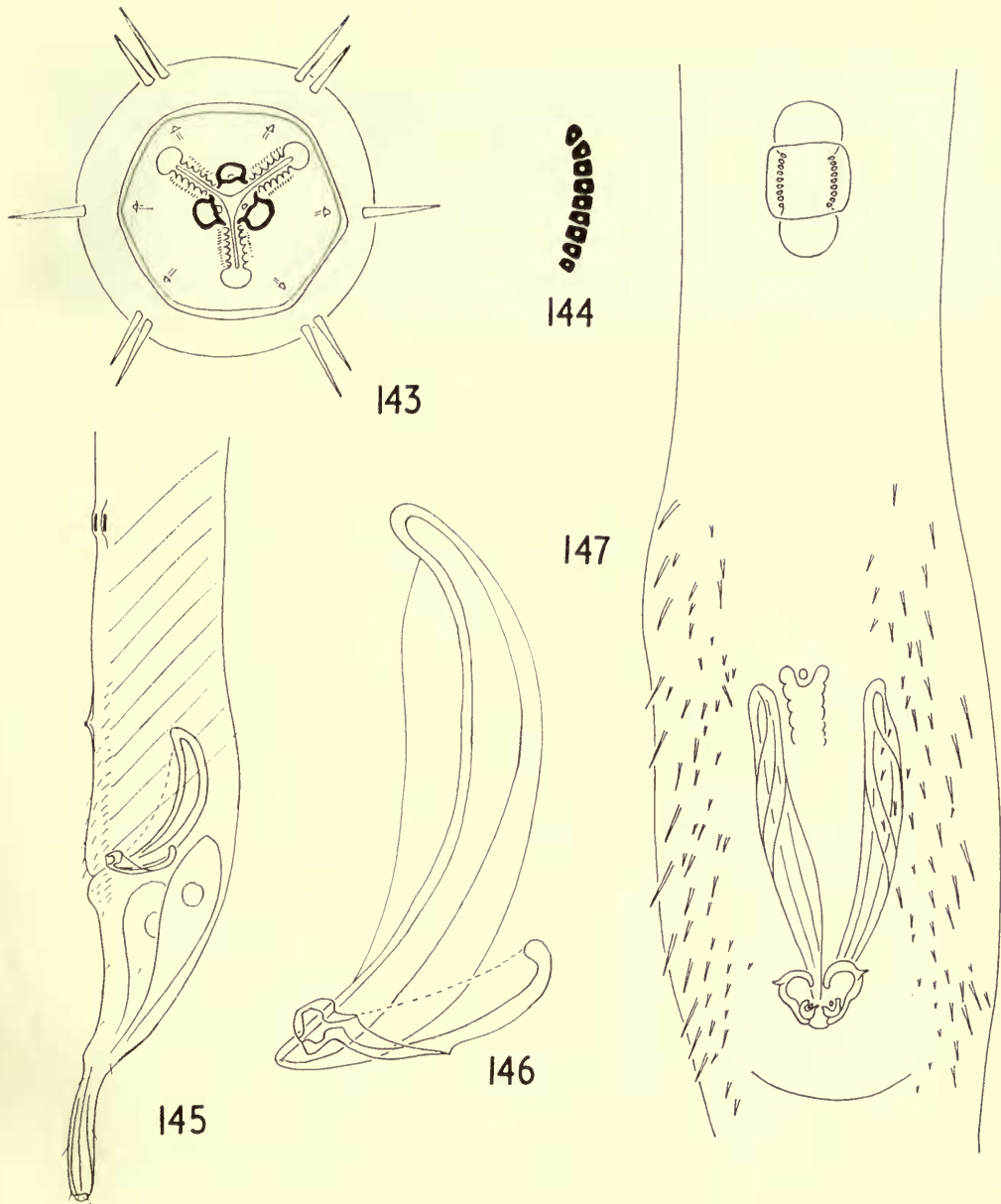


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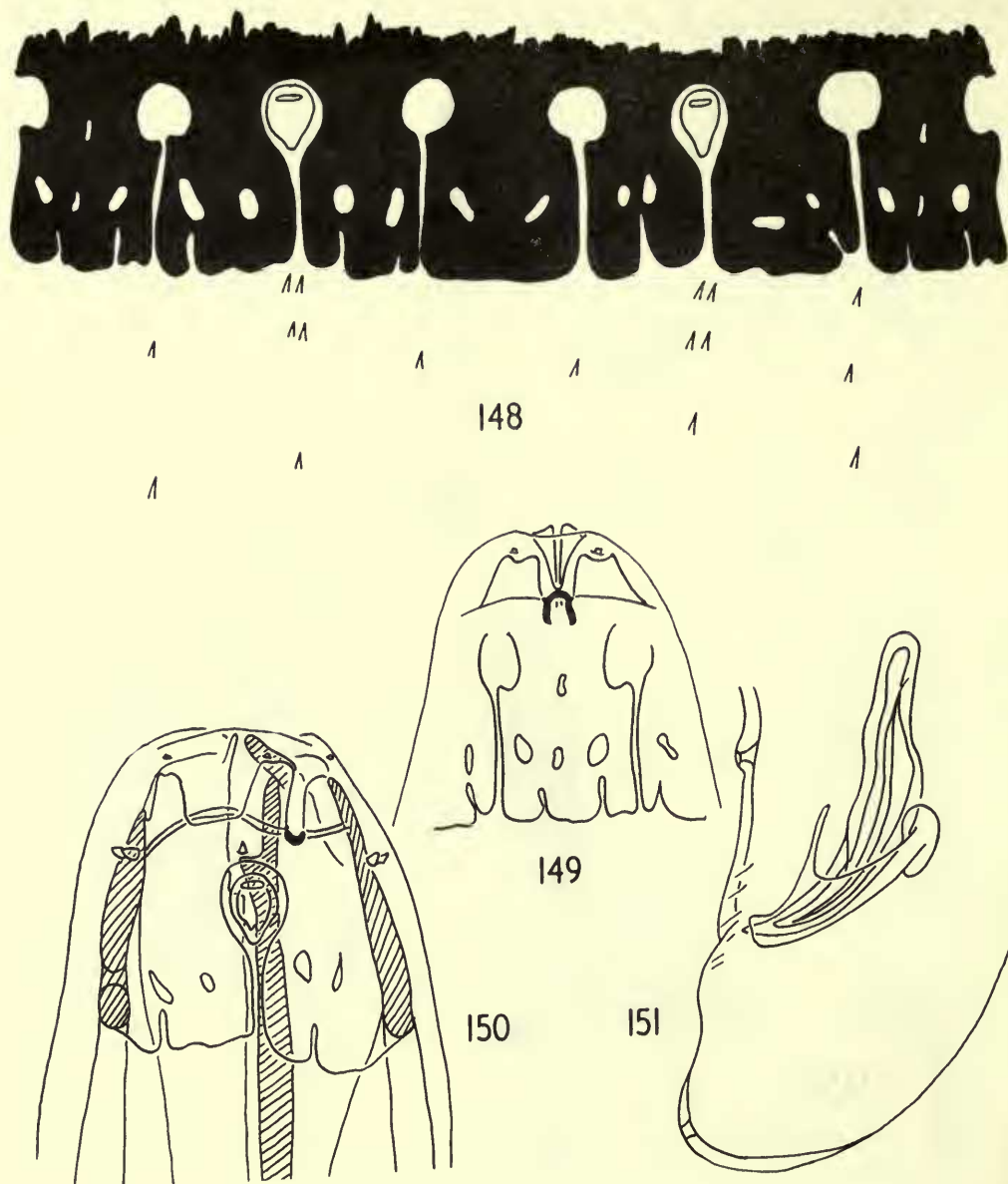


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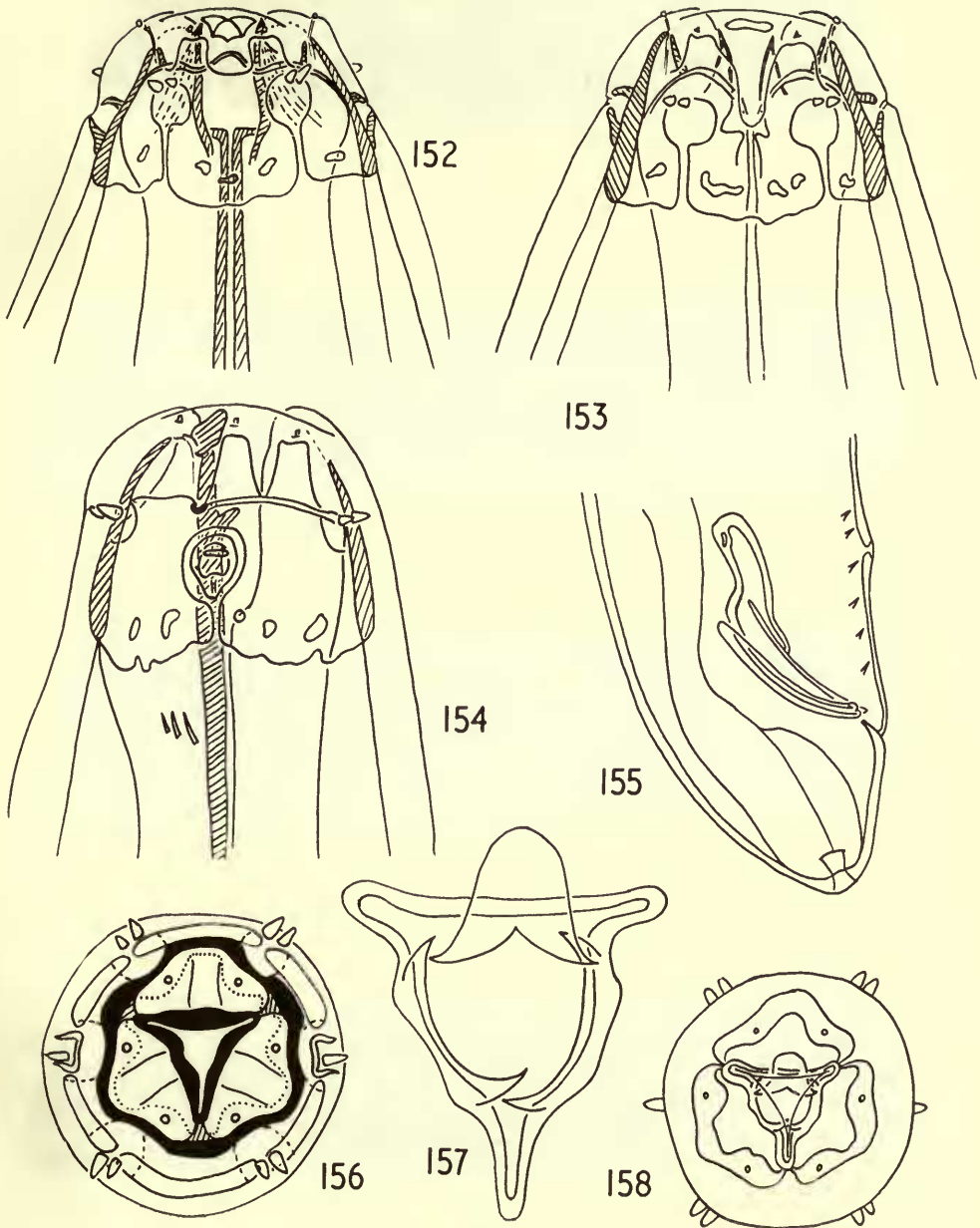
FIGS. 138-142. *Macronchus shealsi*. Fig. 138. Dorsal view of head. Fig. 139. Ventral view of head. Fig. 140. Deep en face view of head. Fig. 141. Lateral view of head. Fig. 142. Lateral view of anterior end of body.



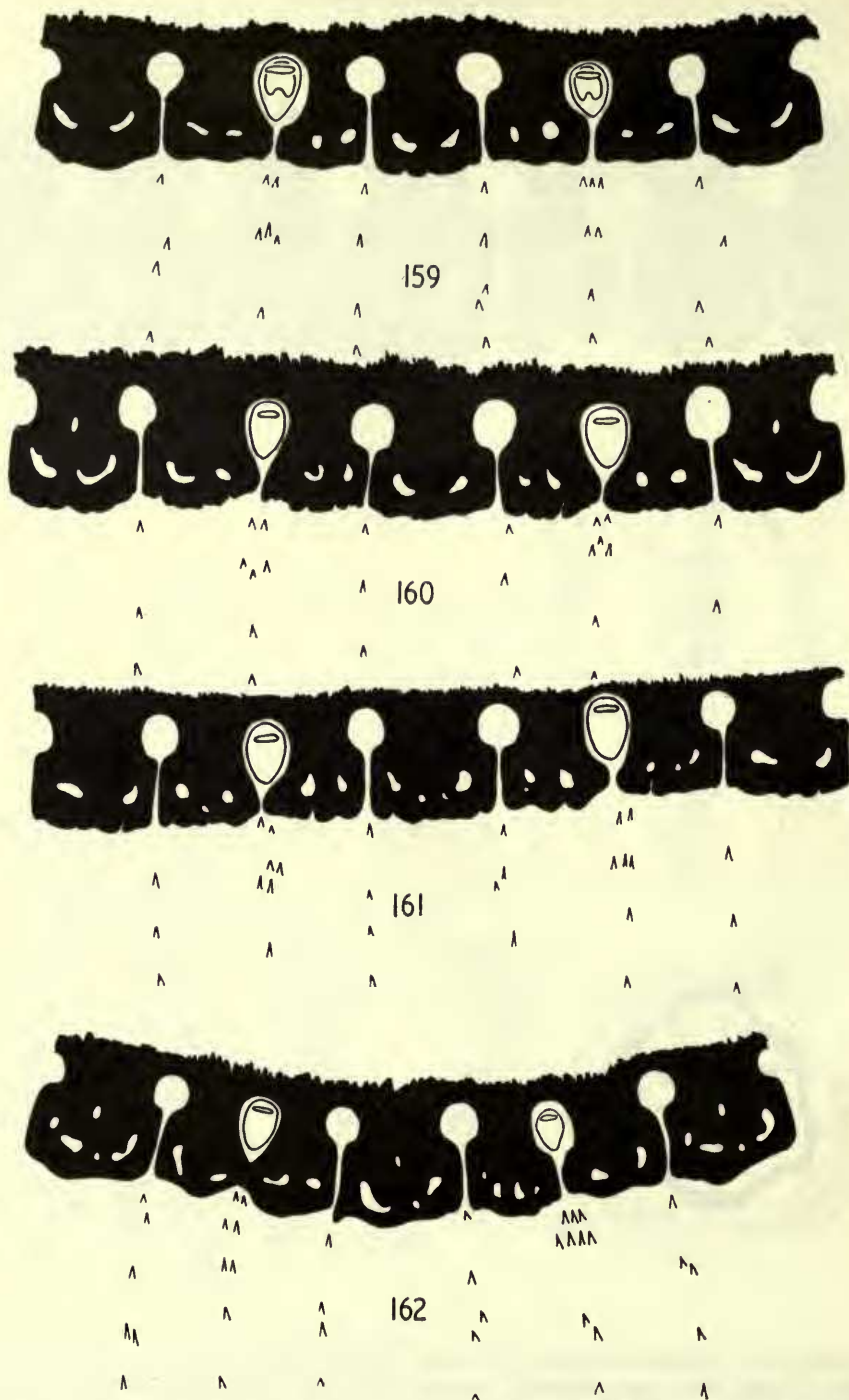
FIGS. 143-147. *Macronchus shealsi*. Fig. 143. *En face* view of head. Fig. 144. Detail of cuticular structure, of one side, in anterior pre-cloacal supplement. Fig. 145. Lateral view of male tail. Fig. 146. Detail of spicules and gubernaculum. Fig. 147. Ventral view of male body anterior to cloacal opening showing distribution of setae and the disposition and appearance of the pre-cloacal supplements. Note the form of the posterior ends of the gubernaculum.



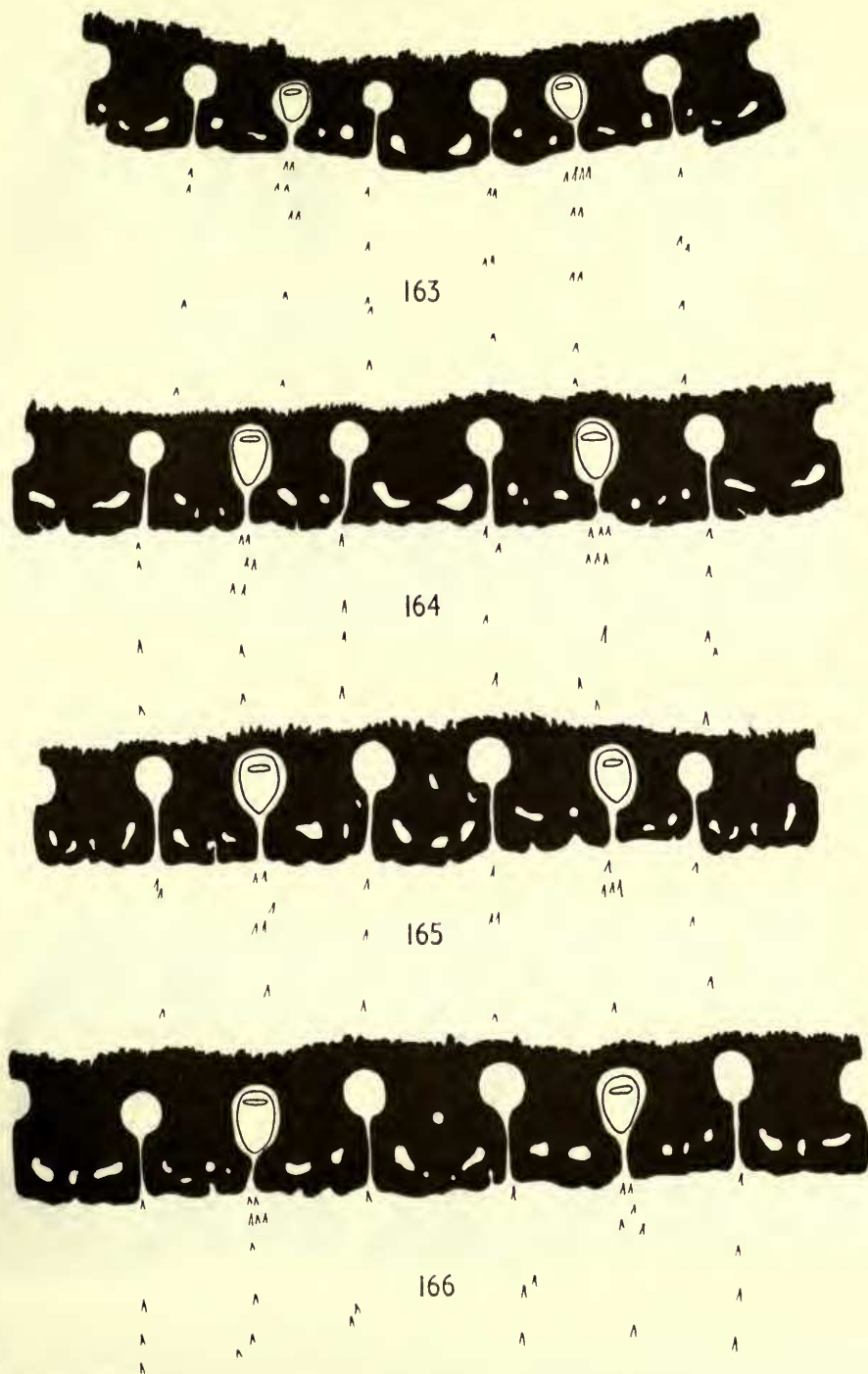
FIGS. 148-151. *Thoracostoma angustifissulatum*. Fig. 148. Posterior part of the cephalic capsule with the ventral lobe at each end and the dorsal lobe in the centre. Anterior edge not in detail. Fig. 149. Ventral view of head. Fig. 150. Lateral view of head with the dorsal surface to the right. Fig. 151. Lateral view of male tail.



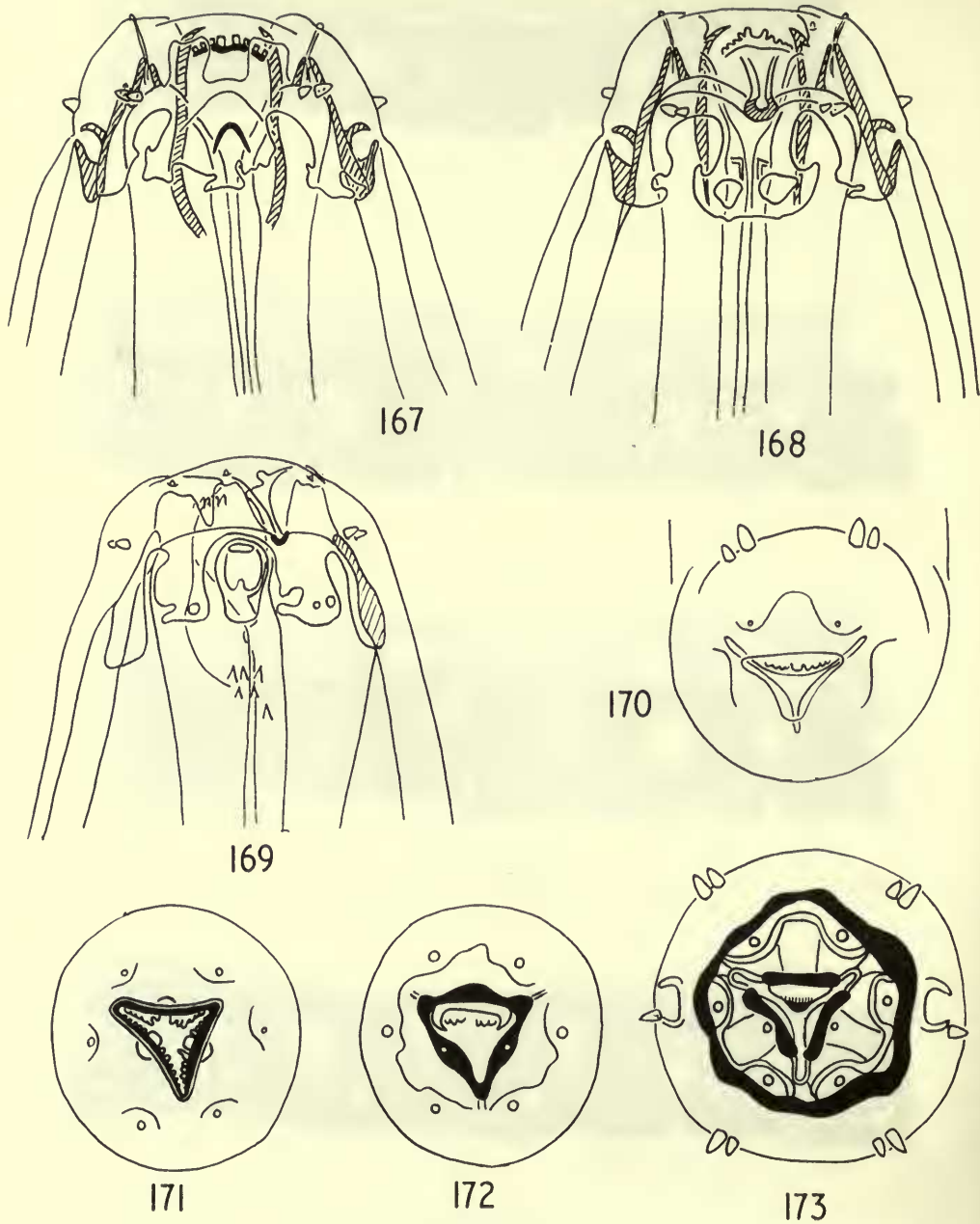
FIGS. 152-158. *Thoracostoma jae*. Fig. 152. Dorsal view of head. Fig. 153. Ventral view of head. Fig. 154. Lateral view of head with the dorsal surface to the left. Fig. 155. Lateral view of male tail. Fig. 156. Deep *en face* view of head. Fig. 157. Sketch of buccal armature. Fig. 158. *En face* view of head, superficial.



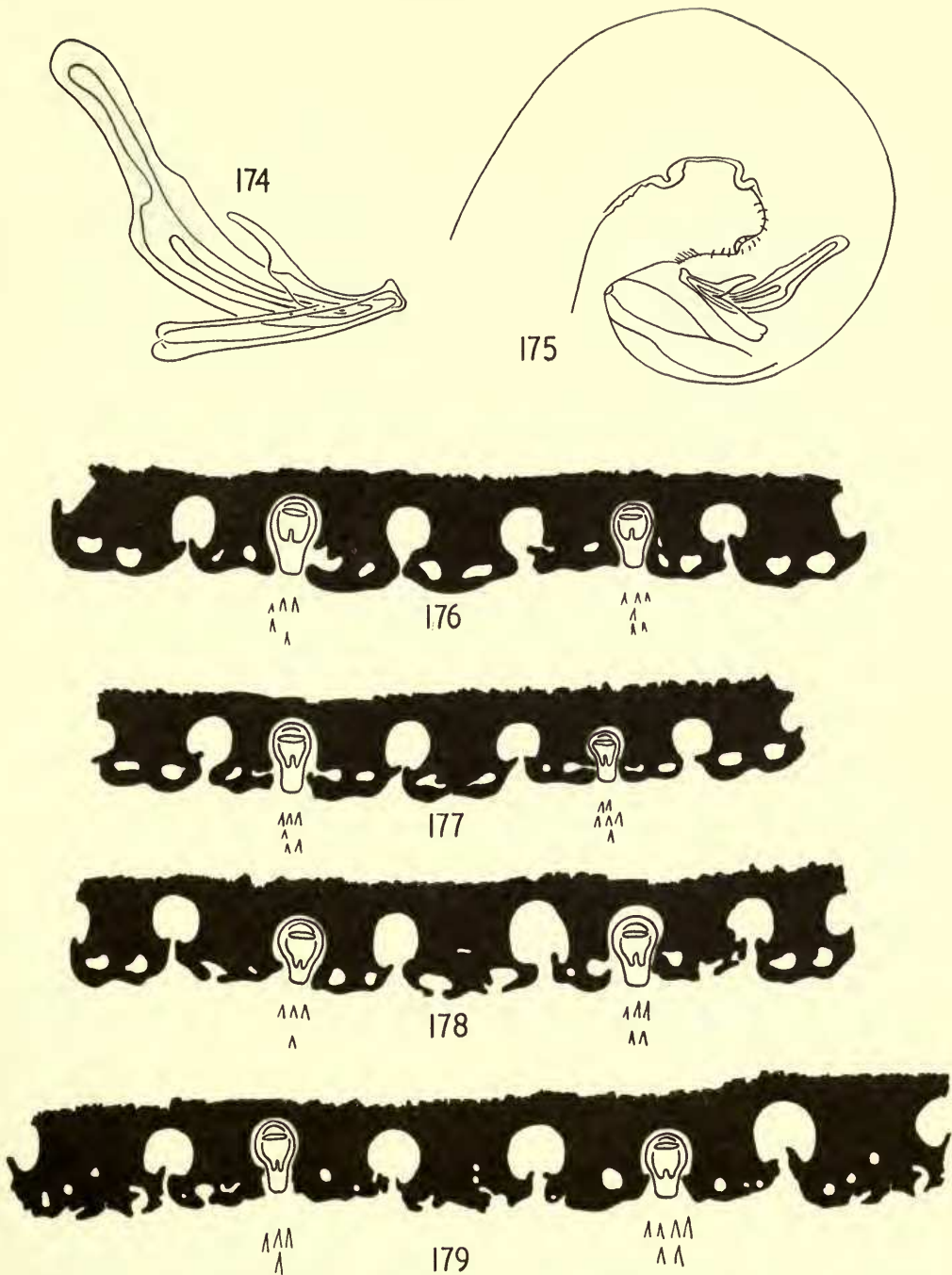
FIGS. 159-162. *Thoracostoma jae*. Detail of posterior edge of cephalic capsule and distribution of nuchal setae with ventral lobe at each side and dorsal lobe in centre. Anterior edge not in detail. All males. Fig. 159. 8.3 mm. body length. Fig. 160. 8.8 mm. Fig. 161. 7.2 mm. Fig. 162. 7.6 mm.



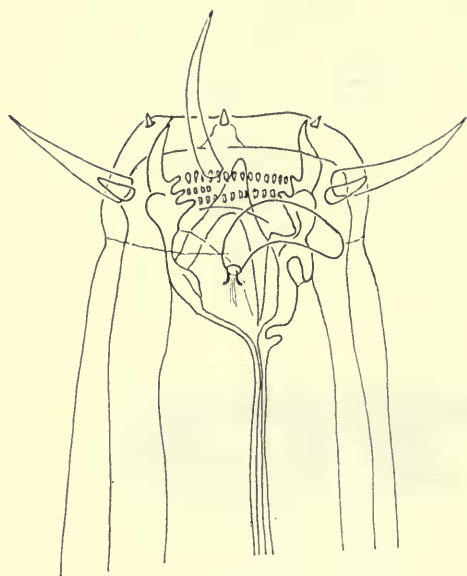
FIGS. 163-166. *Thoracostoma jae*. Detail of posterior edge of cephalic capsule. Anterior edge not in detail. Fig. 163. Larva of 6.9 mm. body length. Fig. 164. Female, 8.4 mm. Fig. 165. Female, 7.4 mm. Fig. 166. Female, 9.0 mm.



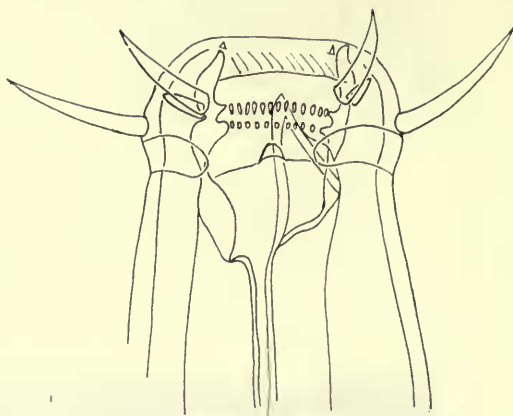
FIGS. 167-173. *Thoracostoma zeei*. Fig. 167. Dorsal view of head. Fig. 168. Ventral view of head. Fig. 169. Lateral view of head with dorsal surface to the right. Fig. 170. Oblique dorsal view of mouth opening. Fig. 171. En face view of head, surface. Fig. 172. The same, slightly below surface. Fig. 173. The same, deep.



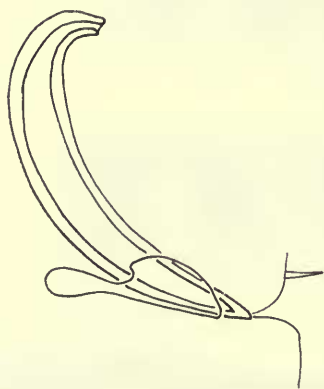
FIGS. 174-179. *Thoracostoma zeae*. Fig. 174. Detail of spicules and gubernaculum. Fig. 175. Lateral view of male tail. Figs. 176-179. Posterior part of the cephalic capsule with the ventral lobe at each side and the dorsal lobe in the centre. Anterior edge not in detail. Figs. 176-178. Larvae. Fig. 179. Male.



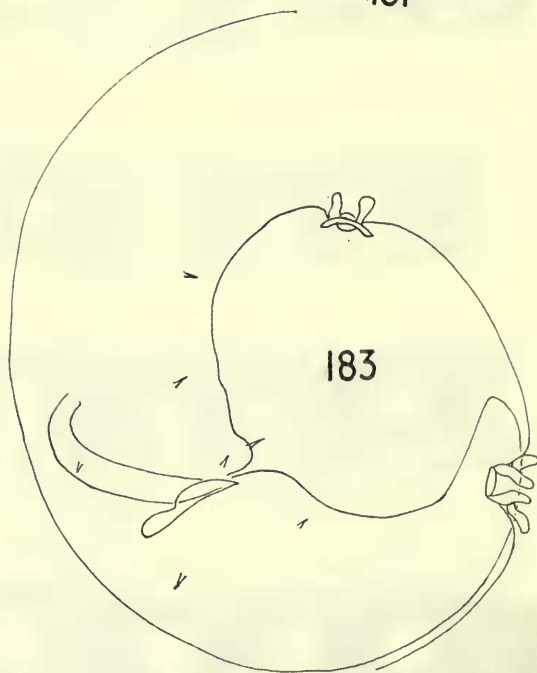
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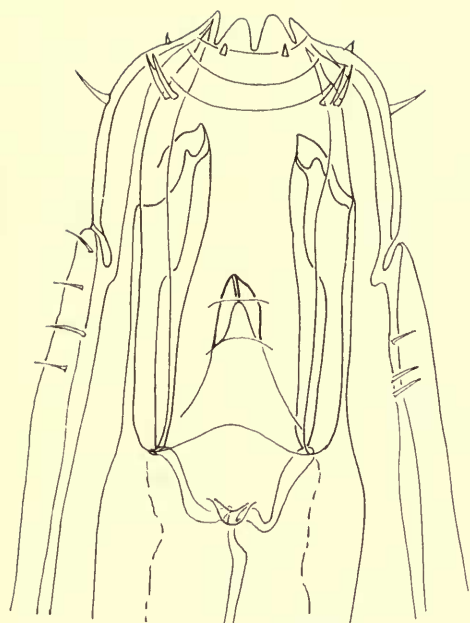


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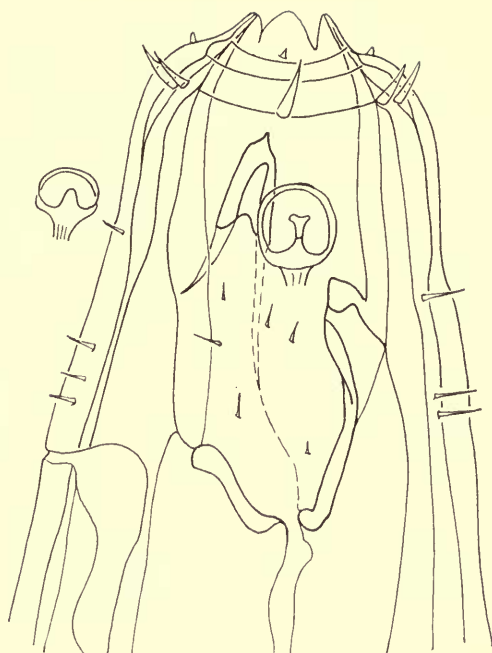


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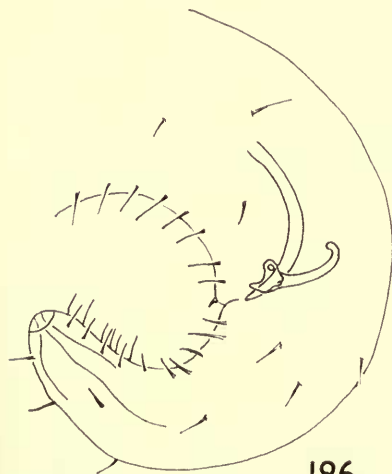
FIGS. 180-183. *Eurystomina sudensis*. Fig. 180. Lateral view of head with the dorsal surface to the right. Fig. 181. Dorsal view of head. Fig. 182. Detail of spicules and gubernaculum. Fig. 183. Lateral view of male tail.



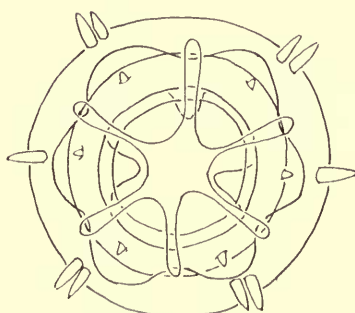
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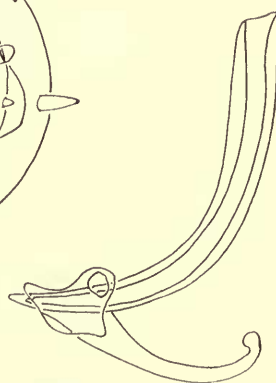
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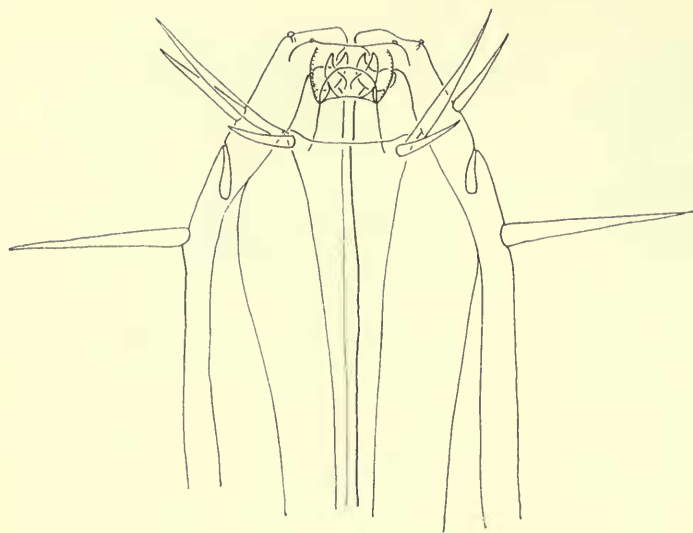


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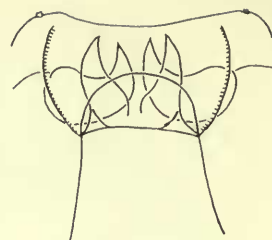


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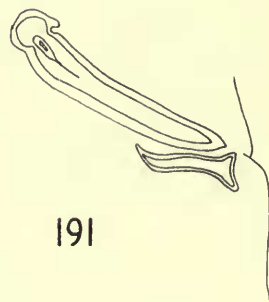
FIGS. 184-188. *Pontonema yaena*. Fig. 184. Dorsal view of head. Fig. 185. Lateral view of head with the dorsal surface to the right. Variant amphid form shown to the left. Fig. 186. Lateral view of male tail. Fig. 187. *En face* view of head. Fig. 188. Detail of spicules and gubernaculum.



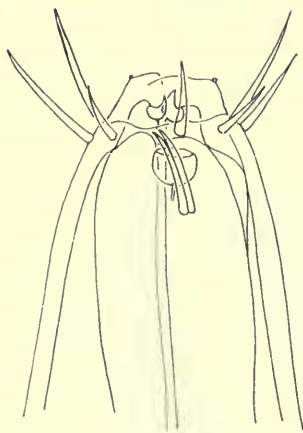
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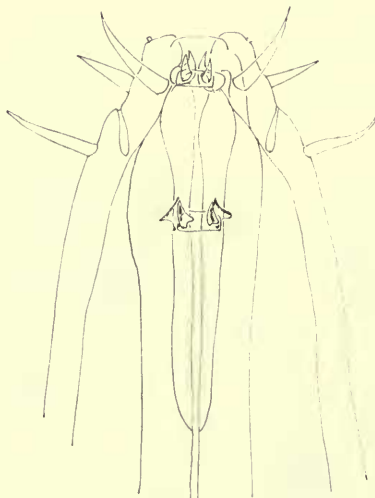
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FIGS. 189-194. *Thalassironus jungi*. Fig. 189. Dorsal view of head. Fig. 190. Detail of buccal dentition. Fig. 191. Detail of spicules and gubernaculum. Fig. 192. Lateral view of anterior end. Fig. 193. Dorsal view of larval head. Fig. 194. Lateral view of male tail.

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